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THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME

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LIFE HISTORY, ENVIRONMENT,
AND MARICULTURE STUDIES OF THE
DUNGENESS CRAB, *CANCER MAGISTER*,
WITH EMPHASIS ON THE
CENTRAL CALIFORNIA FISHERY RESOURCE

Edited by

PAUL W. WILD AND ROBERT N. TASTO
Marine Resources Branch



1983

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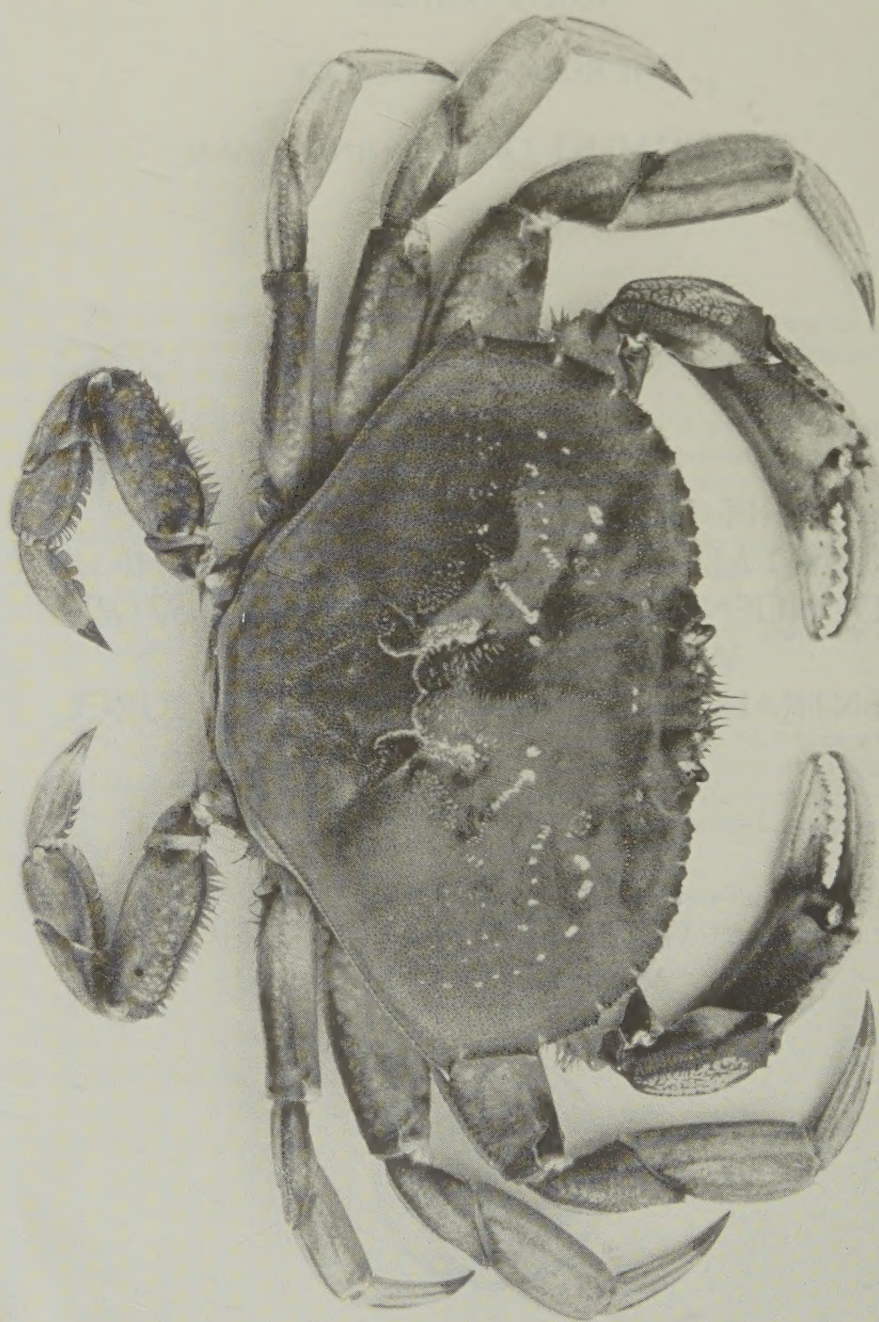


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DEDICATION

This Bulletin is dedicated to Harold G. Orcutt who organized, directed, and guided the Dungeness Crab Research Program from its inception in 1974 until he retired from State service on May 18, 1979.

Hal Orcutt's professional career spanned 38 years. After graduating from Wilson Teachers College, Washington, D.C. with a Bachelor of Science degree in Marine Biology in 1941, he began his career as Marine Investigator for the New Hampshire Fisheries Commission. From 1942 to 1946, Hal served with the U.S. Army including a tour as Fisheries Officer, U.S. Army Military Government Headquarters 8th Army, Japan. Before, during, and after military service, Hal attended several graduate schools including the University of New Hampshire, Harvard University, and lastly Stanford University from which he received his Ph.D. degree in 1949. His career with the California Department of Fish and Game began in 1948 when he became a Jr. Aquatic Biologist at Pacific Grove and culminated in 1967 with an appointment as Laboratory Supervisor in charge of northern California marine investigations headquartered in Menlo Park. Throughout his career, Hal authored a number of scientific and popular articles on fish, shellfish, and fisheries. His affiliation with professional societies includes Phi Sigma Pi (National Honorary Educational), Sigma Zeta (National Science-Math), Sigma Xi (Scientific Research Society), and the American Institute of Fishery Research Biologists.

Hal has always been admired, respected, and considered a friend by his co-workers within the Department and other colleagues in the scientific community. In addition, he is particularly devoted to his family which presently includes his lovely wife Anita, their two children Linda and Robert (a Department of Fish and Game Wildlife Biologist) and their spouses, and three grandchildren.

The successful completion of work which has led to this Bulletin is a tribute to Hal's exceptional scientific and administrative ability.

ACKNOWLEDGMENTS

The success of the many studies presented in this Bulletin would not have been possible without a coalition of effort and support from a wide variety of people, organizations, and agencies. Included are administrators, scientists, technicians, clericals, librarians, boat crews, commercial fishermen, and others to whom we are immensely grateful. It would be difficult in this section to do justice to all without inadvertently slighting or even omitting some. For these reasons, we have chosen to provide a listing of contributors by organization in alphabetical order (Appendix I). In some instances authors of chapters are included where additional substantial contributions were made. To all who have contributed to this research, we extend our heartfelt thanks.

Paul W. Wild and Robert N. Tasto, Editors

ABSTRACT

This report describes the results of the California Department of Fish and Game's Dungeness Crab Research Program (1974-1980) plus several related studies and provides a detailed history of the California fishery. The Dungeness Crab Research Program was developed in response to a severe and sustained decline in central California Dungeness crab landings; this decline is the primary focus of the investigations presented in this report. Research results are presented for life history, environmental, and mariculture studies relating to egg, larval, juvenile, and adult stages of the Dungeness crab. Specific areas of study include stock identification; larval and juvenile dynamics focusing on movement, distribution, relative abundance, age and growth, and predation; impacts of commercial trawl fishing; ocean climate and its effects on life cycle stages and fishery landings; reproduction; pollution such as chlorinated wastewater, toxic trace elements, pesticides and PCB's, and hydrocarbons; and laboratory culture techniques. This report concludes with a summary of the Dungeness crab life cycle and research results and a discussion of management options and further research needs.

Chapter 1

A HISTORY OF DUNGENESS CRAB FISHERIES IN CALIFORNIA

by

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INTRODUCTION

The Dungeness crab, *Cancer magister*, ranges from Amchitka Island in the Aleutians (Hoopes 1973) to the vicinity of Pt. Conception, California. Although the range is often reported to extend to Magdalena Bay, Baja California, the identification as *C. magister* of "two young specimens among miscellanea collected at Magdalena Bay, lower California" (Lockington 1876) presently cannot be verified.

Substantial populations of Dungeness crabs occur along the coast of northern California and the Bodega Bay-San Francisco area. Smaller populations occur in Monterey Bay and the Morro Bay-Avila area. Commercial fishing and some sportfishing for this species are conducted from ports at Crescent City, Trinidad, Eureka, Fort Bragg, Bodega Bay, San Francisco Bay, Princeton, Monterey Bay, Morro Bay, and Avila.

EARLY USE OF DUNGENESS CRABS

Crabs were undoubtedly first utilized as a food source by indians at various locations in California. Although no reference is made specifically to Dungeness crabs, the locations and fishing methods used suggest that Dungeness crabs were being harvested.

Women of the Tolowa Indian Tribe in the Crescent City area combed tidal pools for crabs and used sticks to agitate and unbury them from the sand close to shore (Rita Hayden, Univ. Calif., Berkeley, unpublished manuscript; Greengo 1952).

Yurok Indians of northern Humboldt County and Wiyot Indians in the Humboldt Bay area speared crabs through the carapace with a stick or pole. Sometimes crabs were speared near estuaries of rivers when the crabs were "there to change their shells" (Heizer and Mills 1952).

Greengo reports that the Yurok, Wiyot, and Mattole tribes used a circular frame trap with mesh made from the inner bark of willow; mussels were used for bait. The Yurok also used an open-work twined form of trap. These types of gear apparently are similar to the hoop or ringnets which were used for many years in the commercial fishery and continue to be used in the sportfishery.

Farther south in the Shelter Cove area, Sinkyono Indians caught crabs by hand (Nomland 1936). Wappo Indians were reported to have picked crabs off the

¹ Retired November 2, 1982

beaches north of San Francisco and occasionally to have swum after them (Hayden, unpublished manuscript).

Greengo reports that Wiyot Indians boiled crabs. The Yurok either boiled crabs in hot sand or broiled them on the open fire. The Tolowa cooked crabs in sand.

THE COMMERCIAL DUNGENESS CRAB FISHERY

Early development of the commercial fishing industry in California took place at San Francisco around 1848, just prior to the gold rush, when a group of Italian immigrants began harvesting local fish populations. Growth of the industry was rapid as those who came to seek gold settled in and around San Francisco and turned to other more abundant resources.

Initially, crabs probably were taken incidentally with other fish in nets and seines. Crabs were thought to have been marketed in San Francisco in 1860. By 1863, it is certain that crabs were received commercially at "Meiggs Wharf", an area at the foot of Taylor Street set aside by the California State Legislature for the construction of a wharf (Hayden, unpublished manuscript).

In 1870, the California Fish Commission was created by the Legislature for the restoration and preservation of fish in the waters of the State. Official records of commercial fisheries were started by the Commission during the same year.

In 1870, Captain E. Wakeman of the Commission made a survey of the fisheries of San Francisco Bay. He reported that in Sausalito Bay, Italian fishermen, who were fishing for smelts, soles, flounders, sardines, and anchovies, would sometimes catch nothing but crabs. Crabs which damaged the nets so irritated the men that they were inclined to leave them on the beach to die. Crabs were in fact the only thing that was left on the beach; all kinds of fish were taken or returned to the water.

In 1880, the United States Commission of Fish and Fisheries made a survey of the fisheries of the Pacific Coast. At that time, San Francisco apparently was the only place where Dungeness crabs were marketed regularly (Rathbun 1887). Fishing was taking place on the sandy beaches on the San Francisco side of the Bay, especially on the south side of the Golden Gate, between the city and the sea. Dungeness crabs were caught in immense numbers in seines, together with red crabs, *Cancer productus*, rock crabs, *Cancer antennarius*, and many shallow-water species of fish. The same species of crabs were also caught off the wharves and piers in San Francisco Bay in crab nets baited with fish and offal. The red and rock crabs were not marketed, but were thrown back into the sea or left on the shore to die. Rathbun reported that, in spite of the great numbers of Dungeness crabs which were constantly being taken and the reckless manner in which the catch was wasted by most of the fishermen, the supply had not yet diminished perceptibly. Rathbun also noted that fewer crabs were brought to market in winter than in summer. Three or four good-sized crabs sold in the markets at retail for \$0.25. There was no size restriction or export trade in crabs. Annual sales of crabs in the San Francisco markets were thought to be about 300,000 by count, weighing an average of 1 lb each (about one-half the weight of legal-sized crabs of today), with a value to the fishermen of about \$15,000. Fishing for crabs inside the Bay did not persist long after 1880, because the crabs were small and eventually too inadequate in number to satisfy the demand.

Sailboats and row boats were used in the fishery for about 25 to 30 years. Many of the boats were built by F. Castagnola Company, located at Battery and Union Streets. During this period there was rising demand for sailboats which were specially designed for crabbing. These were probably lateen boats and were characterized by a triangular sail extended by a long spar slung to a low mast; they were called "ceilagnos". Their beam was wide, the stern high and pointed, and a removable bowsprit was attached to the bow. In 1885, steam-power engines were introduced, causing replacement of some sailboats by 1892.

During the early years of the fishery, Italian fishermen started to make use of the hoopnet or ringnet for catching crabs (Figure 1). This type of net consisted of two iron hoops, one measuring 30 to 36 inches in diameter and made of $\frac{1}{2}$ -inch round iron rod, and the other 15 to 18 inches in diameter and made of $\frac{3}{8}$ -inch round iron rod. The lower hoop was reinforced with three to six spokes. The spaces between the spokes were interlaced with netting, which like that on the sides was supposed to be coarse enough to permit escapement of undersized crabs to make the net easier to pull. To the center of the spokes, a hemispherical cap of woven wire was lashed to enclose the bait. The bait usually consisted of small fishes taken by seines in the Bay. The bait was placed under the wire cover which prevented it from being eaten too rapidly by crabs. A bridle of three lines was attached from the large hoop to a single line, 70 to 150 ft in length, to which a float was attached to mark the location of the hoopnet while it was being fished. The floats were made of cedar, cork, or copper. The hoopnet was the primary type of gear used as the crab fishery moved out of the Bay.



FIGURE 1. Dungeness crab hoopnets. Photo by J. B. Phillips, 1934.

According to Weymouth (1916), hoopnets were fished outside the Golden Gate in depths of 5 to 10 fm.¹ A series of about 20 nets was thrown overboard, one at a time, as the boat ran slowly against the tide. After setting, the fisherman waited a half hour or more before pulling the nets. To lift the gear, the boat again was run slowly against the tide, the float was caught and lifted aboard, and the line carefully coiled in until the boat was above the net which was then raised quickly and drawn to the surface. The crabs were sorted; those of marketable size were put into a compartment in the stern and the remainder thrown overboard. The boats usually went out to the fishing grounds early in the morning and were at work by sunrise. The nets were hauled at intervals of a half hour or more until the early afternoon when the boats would return to unload their catch.

According to Wilcox (1902), boats with small gasoline engines (5 horsepower) started to take the place of sailboats from 1895 to 1899. During 1899, 49 sailboats and 33 gasoline boats were used in the crab fishery. By 1904, there were 109 gasoline boats in the fishery. The gasoline boats, with two men, fished 20 to 30 ringnets each; the sailboats averaged 15 nets, with one or two men. The catch was nearly all made outside the harbor where crabs were still plentiful and larger than those found in the Bay. In 1899, the crab grounds extended from the mouth of the Golden Gate along the north shore about 10 miles, and the same distance along the beaches to the south. With favorable weather, crabs were fished year-round. At this time, crabs that were brought to market averaged 30 lb per dozen. Prices fluctuated between \$0.40 and \$1.25 per dozen with the average about \$0.70.

As a result of increasing boat speed and maneuverability, coupled with more manpower from immigrant fishermen, the crab catch began to increase. The first crab landing statistics were furnished by the U.S. Commission of Fish and Fisheries. Crabs were reported in dozens. In 1888, 77,800 dozen or 933,600 crabs were landed. In 1889, crab landings were first reported by weight and 1,944,000 lb were landed. Landings increased steadily each year, and in 1892, 2,750,000 lb were landed. Landings were also made in Humboldt County in northern California and these ranged from 86,400 lb in 1889 to 112,320 lb in 1892. Landings in San Francisco County in 1895 were 2,565,000 lb, and in 1899 were 3,664,680 lb. In 1904, the landings took a big jump to 5,110,500 lb, valued at \$154,738 to the fishermen. The fishermen continued to be mostly Italians. The average catch was about five dozen crabs per day and the average weight per crab was between 2 and 3 lb. In 1904, four steamers fishing out of San Francisco with Mediterranean paranzella nets (Scofield 1948), introduced into the trawl fishery in 1876 (Jordan 1887), accounted for 4% of the landings. Landing figures are not available from 1905 through 1913, but the State Board of Fish Commissioners reports indicated that landings apparently decreased.

According to a report from the State Board of Fish Commissioners for the years 1895–1896, the supply of crabs was equal to the demand and landings were still increasing at that time; however, it was believed that crabs were gradually becoming more scarce because the fishermen had to go a greater distance for their catch. It was suggested that this branch of the fishing industry should receive the attention of the Legislature and recommendations of the State Board of Fish Commissioners to help restore the fishery. The first legislative protection for crabs was a law enacted in 1897 prohibiting the possession and sale of female Dungeness crabs. Concern was voiced in the Commissioners'

¹ One fathom (fm) = 6 ft.

report of 1901–1902 that the crab fishermen, who used gasoline boats in supplying the markets, fished so extensively that the law prohibiting the take and sale of female crabs was not sufficient because the supply of crabs was rapidly decreasing, especially in the vicinity of San Francisco. This scarcity had become so acute that some fishermen began to violate the only provision of State law protecting crabs, the prohibition of capture and sale of females. Apprehension and conviction of two of the principal violators of this law cured the situation rapidly. Several conservation-minded fishermen, recognizing the growing scarcity of crabs, were reported to have asked the Commissioners for a closed season or some additional protection for crabs to prevent the industry from being ruined.

In 1903, a closed season from September 2 through October 31 was established by the State Legislature. In 1905, a minimum size limit of 6 inches, measured straight across the widest part of the back from point to point of the spines, was enacted. In 1909, the open season was shortened to the period from November 1 to March 1. In 1911, based on a recommendation from biologist F.W. Weymouth, the minimum size limit for males was increased to 7 inches, measured over the curve of the widest part of the back from point to point. This greatly eliminated the possibility of females being taken illegally because females seldom attain that size. In 1915, the minimum size limit became 7 inches measured straight across the back. In 1914, the open season was changed to November 16 to August 14. Since that time, the fishing season has been changed numerous times (Tables 1 and 2). The general trend has been to prolong the closed fishing season during the period when the males are molting. This allows their shells to harden and the meat to fill out to an acceptable market condition before harvesting. Since 1929, the opening date of the season in northern California usually has been from 2 weeks to 1 month later than in central California because crabs harden and fill out later in colder northern ocean waters.

TABLE 1. Commercial Fishing Seasons for Dungeness Crabs in Northern California * 1903–1983

<i>Year</i>	<i>Open season</i>	
1903–1909	Nov. 1–Sept. 1	Statewide
1909–1914	Nov. 1–March 1	Statewide
1914–1915	Nov. 16–Aug. 14	Statewide
1915–1929	Nov. 15–July 30	Statewide
1929–1949	Dec. 15–Aug. 30	
1949–1951	Nov. 15–July 31	Statewide
1951–1955	Dec. 15–July 31	
1955–1957	Dec. 15–June 30	
1957–1965	Dec. 15–July 15	
1965–1967	Dec. 8–July 15	
1967–1971	Dec. 1–July 15	
1971–1979	Dec. 1–Aug. 31	
1979–1983	Dec. 1–July 15 †	

* Southern border of Mendocino County north to the Oregon border.

† The Director of the Department of Fish and Game may extend the season up to Aug 31 in any district or portion thereof if written findings of the Department do not conclude that such extension will harm the resource.

TABLE 2. Commercial Fishing Seasons for Dungeness Crabs in Central California * 1903–1983

Year	Open season	
1903–1909.....	Nov. 1–Sept. 1	Statewide
1909–1914.....	Nov. 1–March 1	Statewide
1914–1915.....	Nov. 16–Aug. 14	Statewide
1915–1935.....	Nov. 15–July 30	Statewide until 1929
1935–1949.....	Nov. 1–Aug. 15	
1949–1955.....	Nov. 15–July 31	Statewide until 1951
1955–1961.....	2nd Tues. in Nov.–May 31	
1961–1983.....	2nd Tues. in Nov.–June 30 †	

* Statewide south of the southern border of Mendocino County.

† Since 1979, the Director of the Department of Fish and Game may extend the season up to Aug 31 in any district or part thereof if the written findings of the Department do not conclude that such extension will harm the resource.

Legislation was enacted during the early years of the fishery for licensing of boats, fishermen, and dealers. In 1887, legislation required the licensing of all fishing boats and, in 1909, licensing of commercial fishermen was authorized. In 1911, another law required wholesale fish dealers to obtain licenses and record their transactions. These records were required to be kept by the dealers and to be made available for inspection by Fish and Game deputies.

Another legislative act in 1915 required wholesale fish dealers to submit monthly statements showing the transactions of the preceding month. This system was altered in 1917 by legislation which required dealers to record all receipts of fish transactions in duplicate. These records were to specify the weight in pounds by variety and the price per pound, in addition to the information previously required.

The only essential change since 1917 came 2 years later when records of transactions were required in triplicate on forms issued by the State. The triplicate copy was pink and the statistical system became known as the "pink ticket" system. Since 1950, these records have been made out in quadruplicate. The "pink ticket" system has provided a record of fish landings and, since 1915, annual detailed statistics of the California commercial catch have been kept.

The statistical records show that Dungeness crab landings have varied considerably throughout the State although certain patterns are obvious (Figure 2). From the beginning of the fishery until the 1944–45 season, the San Francisco area produced the highest crab landings in California. Beginning with the 1945–46 season, the northern California area generally has been the major contributor to crab landings in the State. Monterey Bay and Morro Bay-Avila areas have never produced significant amounts of crabs. Since the early 1960's, all central California ports have experienced unprecedented low landings. These changes in landings patterns have been due primarily to three factors: (i) changes in regulations, (ii) improvements in fishing methods, and (iii) fluctuations in crab abundance.

In 1917, a State law was enacted which prohibited the shipment of Dungeness crabs outside of the coastal districts between the Oregon border and the Mendocino-Sonoma County line. This law supplanted county ordinances imposed the same year, prohibiting export of crabs. Before the export laws were in effect, as many as 65 boats per season operated in this region (Eureka and Crescent City). Many of these boats came from San Francisco. Phillips (1935) reports that during the 1930's only about eight boats fished regularly out of Humboldt Bay throughout the season. The fleet was augmented to about 20 by some of the

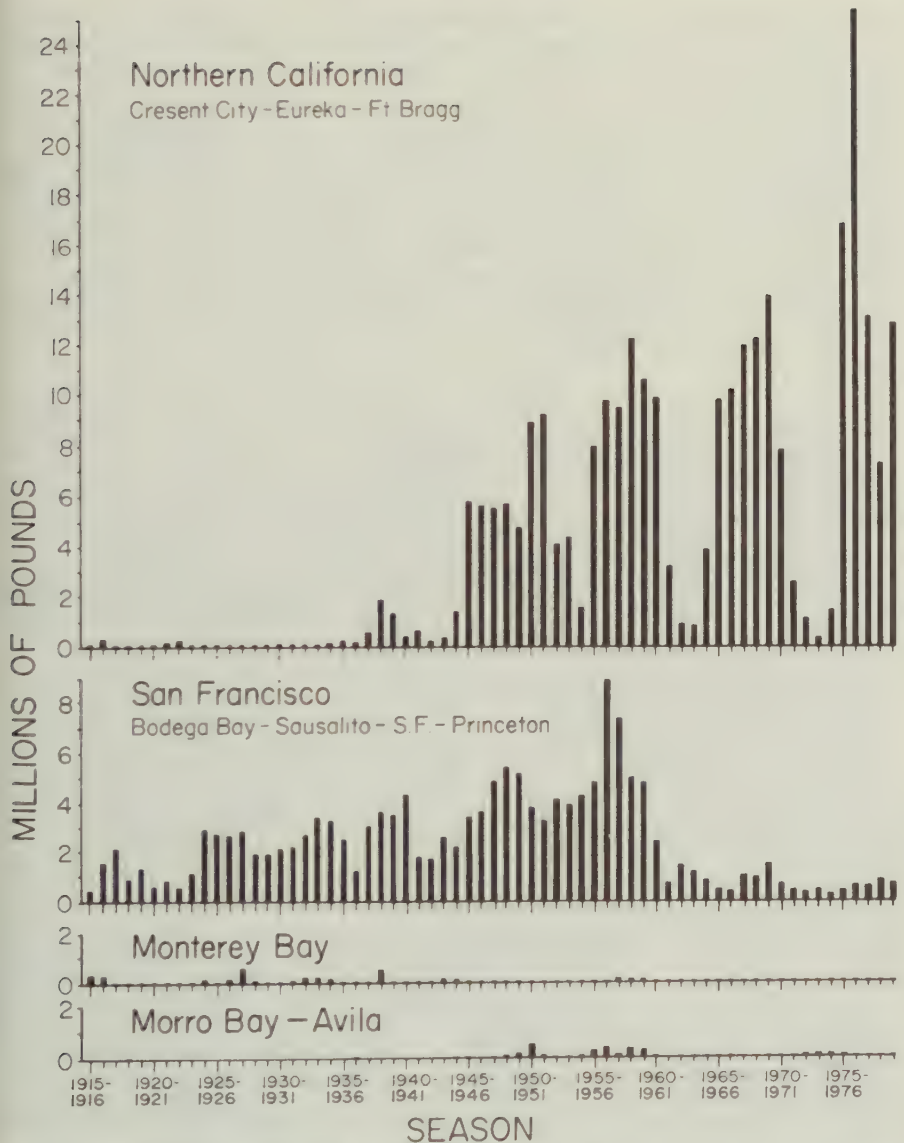


FIGURE 2. Commercial landings of Dungeness crabs in California by area for seasons 1915-16 through 1979-80.

salmon trolling boats that fished crabs during the closed season for salmon. This fleet, no doubt, satisfied the local demand and some crabs were shipped to Crescent City. Approximately three crab boats operated out of Crescent City, but did not fish steadily.

From 1918 to the early 1960's, approximately 200 to 250 boats in the San Francisco area fished crabs each year. The typical boat during this period was an "ordinary jig boat" that could also be used for other types of market fishing

(Phillips 1935). With certain minor additions of labor-saving devices, it was used for fishing crabs. The most popular type of boat was the "Monterey style", distinguished by its clipper bow, with a wide flare forward and a broadly pointed stern (Figure 3). These boats varied in length between 20 and 35 ft, with an average beam of about 8 ft, and were powered by one- or two-cylinder gasoline engines that ranged from 6 to 12 horsepower. A small engine control pit was located near the tiller and a little astern of amidships. A tiny house or shelter was built over the engine control pit. The house was open at the rear and served as protection from spray and wind. All crabbing operations were performed from this engine pit when hoopnets were used. Some of these boats remain in the San Francisco fishery to this day. Boats used regularly in the Eureka area for crab fishing were jig boats, 20- to 40-ft long, with gasoline engines of 8 to 16 horsepower.



FIGURE 3. Monterey style crab boats at San Francisco's Fisherman's Wharf, 1934. Photo by J. B. Phillips.

A 4- to 5-inch powered drum (gurdy) came into use during the early years of power boat operations (Figure 4). This small drum enabled the fishermen to pull their gear faster and more effectively. The drum was placed about a foot above deck on the starboard side of the boat and was operated by a chain drive takeoff from behind the flywheel. It was engaged by a foot clutch. In addition to the small drum, a small deep-grooved iron block (pulley) on an iron-bar davit arm completed the crab hoopnet pulling equipment. The line from a hoopnet

was placed over the pulley and looped around the drum. The drum pulled the net while the fisherman coiled the loose end of the line.

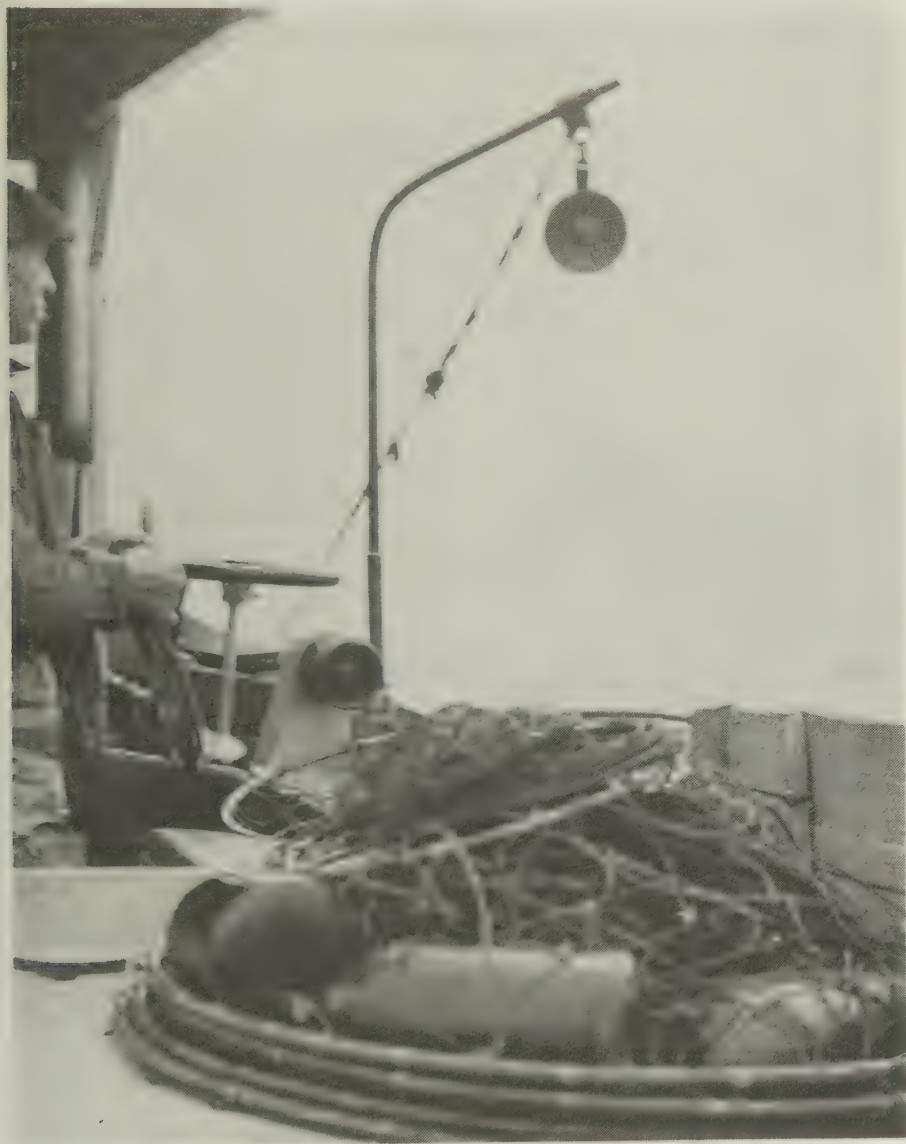


FIGURE 4. Dungeness crab hoopnet pulling equipment. Note pulley at upper right center and powered gurdy at lower left center. Photo by J. B. Phillips, 1934.

Live-boxes were part of the equipment of crab fishermen for many years. Each fisherman had a floating live-box tied to the wharf where he berthed his boat (Figure 5). In the San Francisco area, the box's outside dimensions were generally 2 x 4 x 6 ft and they were constructed of $\frac{3}{4}$ x 3 $\frac{1}{2}$ -inch slats spaced about $\frac{3}{4}$

of an inch apart. Capacity was approximately 35 dozen crabs, but usually not more than 20 or 25 dozen were kept at one time. Live-boxes in the Eureka area were larger than those in the San Francisco area. The smallest was $2 \times 4\frac{1}{2} \times 9$ ft and held about 60 dozen crabs; the largest held about 150 dozen, but the boxes were not kept more than about half full. The fishermen usually emptied the boxes in about 4 days to insure active crabs.



FIGURE 5. Floating crab live-boxes at San Francisco wharf. Photo by W. A. Dahlstrom.

At that time, the market demand for crabs had not kept pace with the increase in numbers of fishermen. The use of the live-box enabled a fisherman to hold several days' supply at one time without duplicating the expense that going out each day would entail. When the fisherman returned to port, he would drop the live crabs in the live-box where they would remain until market orders came in. A supply of crabs could also be carried over a period when rough weather prohibited fishing.

In 1923, holding crabs in live-boxes was prohibited in Del Norte, Humboldt, and Mendocino Counties. The purpose of this regulation was to prevent fishermen from accumulating large quantities of crabs at one time and to discourage smuggling from these areas, a common practice during the early days of the fishery.

Since about the middle 1950's, the use of fishermen's live-boxes has ceased. Dealers have been keeping surplus crabs alive in crab crates or boxes which are floated in the water near receiving stations. A hoist lifts the crates to and from the water. Dealer imposed limits also regulate the supply of crabs.

From the early years of the fishery, it was illegal to pickle, can, or preserve crabs. In 1935, this law was amended to allow fresh crab meat to be preserved in not less than 5-lb containers under refrigerated conditions. In 1938, the courts rendered a decision that crabs caught outside the 3-mile limit were not subject to State law which prohibited shipment of crabs from the Del Norte-Humboldt-Mendocino district. The establishment of crab meat packing plants in Eureka, starting with the 1938-39 season, helped create an increasing market demand in that area. In 1941, State law was changed so that crabs caught anywhere in this district could be exported. Also, the no-canning law was eliminated that year. These factors undoubtedly contributed to the steadily increasing catch in northern California in the following years (Figure 2).

The more efficient crab trap or pot (Figure 6) was introduced in the Crescent City-Eureka area about 1938 and started a conversion from hoopnets. During the period 1939 to 1943, hoopnets were declared the only legal fishing gear in the San Francisco districts. Crab traps were not prohibited in the other crabbing areas. Crab traps were legalized in the San Francisco area in 1943 and several

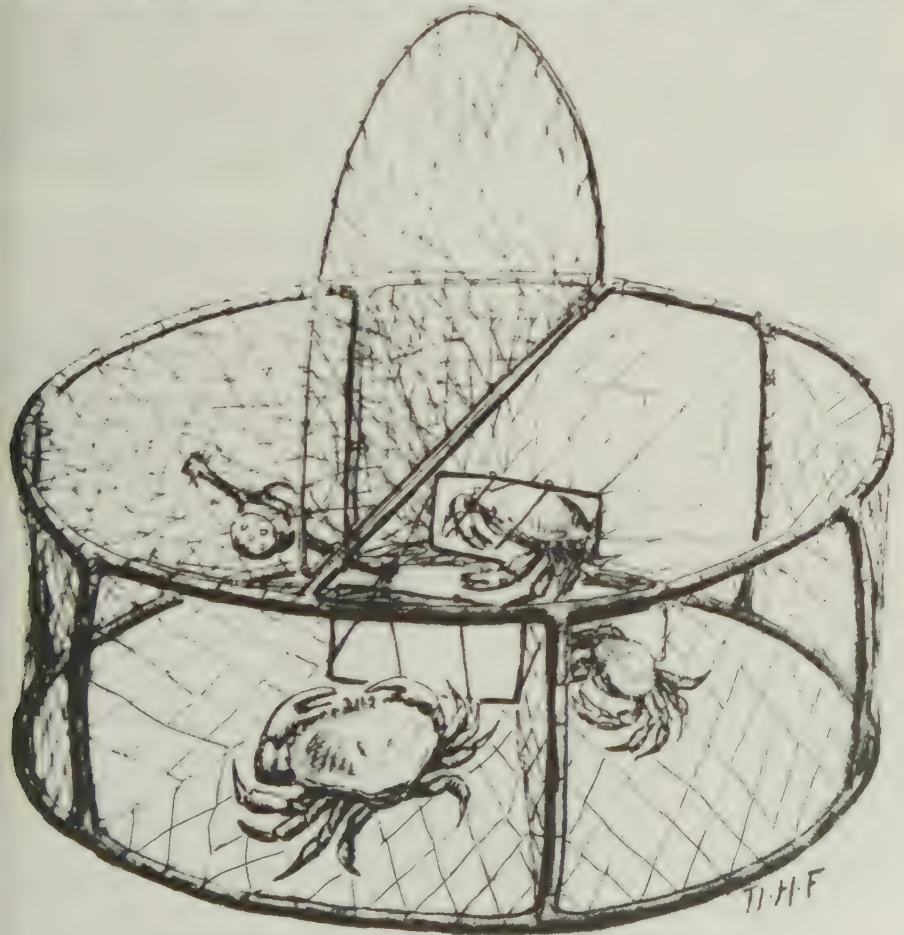


FIGURE 6. Dungeness crab trap. Illustration by D. H. Fry, Jr.

fishermen began using them. The number of fishermen changing from hoopnet to crab traps continued to increase and by 1947, the bulk of the crab catch was being taken by traps. At Bodega Bay, the changeover to the exclusive use of traps probably occurred in 1945 or 1946. Crab traps are used exclusively in the commercial fisheries today.

The Dungeness crab trap is usually a circular, iron frame covered with coarsely woven, taut stainless steel wire mesh with two entrance tunnels directly opposite each other (Figure 6). The tunnels are fitted with trigger bars to prevent escapement. Strips of rubber innertube are wound around the iron bars of the frame before the wire mesh is applied to minimize deterioration from electrolysis. A hinged lid covers half of the top ring and a bait container is secured between the entrance tunnels. The most commonly used baits are squid placed in bait containers and (or) fish carcasses suspended between the tunnels on bait hangers. Other baits used are clams, herring, and mussels. Present day crab traps range from about 36 to 48 inches in diameter with the most popular trap being 40 inches.

Traps generally are set in a straight line about 200 to 300 ft apart. First, the buoy and line are trailed off the stern of the vessel underway at about half speed; then the trap is pushed (set) off the stern. Some fishermen, in order to get the desired spacing between traps, time the interval between setting traps. As many as 50 to 100 traps may comprise a string of traps, which may extend several thousand feet. The spacing is sufficient to allow for pulling, emptying, rebaiting, and resetting a trap while the boat runs along the string.

The traps generally are fished from 1- to 10-day periods depending upon the time of year, weather and ocean conditions, and abundance of crabs. Fishing depths vary from 2 to 50 fm but are most frequently from 20 to 35 fm.

The heavier gear and the need to haul large numbers of traps to and from the fishing grounds resulted in a change to larger more powerful boats with diesel engines (Figure 7). A 1968 survey indicated that the typical crab boat was about 36 ft (range: 28 to 50 ft) in length in the San Francisco area and about 40 ft (range: 30 to 60 ft) in northern California. Engines ranged from 20 to 465 hp and averaged about 120 hp. These are typical of boats presently used in the crab fishery. Many crab fishermen also troll for salmon and (or) albacore when crabbing is slow or the crab season is closed.

A new and more efficient method of pulling traps, the hydraulic power block was initiated in the early 1960's (Figure 8). Polypropylene and polyethylene line also made their appearance in the early 1960's. The flexibility, light weight, and long life was a decided improvement over the previously used manila rope. Another innovation was the use of styrofoam, sponges, or other similar lightweight materials for buoys.

Live-tanks for holding crabs aboard vessels currently are common in northern California and some vessels use them in the Bodega Bay area. These tanks usually are made from iron plates welded together to fit in the hold of the vessel (Figure 9). A screen is used on some vessels to facilitate recovery of crabs from the tank. It is hoisted from the bottom of the tank, lifting the crabs as it rises. Crabs cared for in this manner are in good condition when unloaded at the dock.

In the Monterey Bay crab fishery, trammel nets, which were developed to catch fish, were used to catch crabs in the early 1900's. As described by Phillips (1935), the trammel net had three walls of webbing hung between a common



FIGURE 7. Dungeness crab boats at anchor in Bodega Bay, 1970. Photo by W. A. Dahlstrom.



FIGURE 8. Hydraulic power block for lifting Dungeness crab traps. Photo by W. A. Dahlstrom.

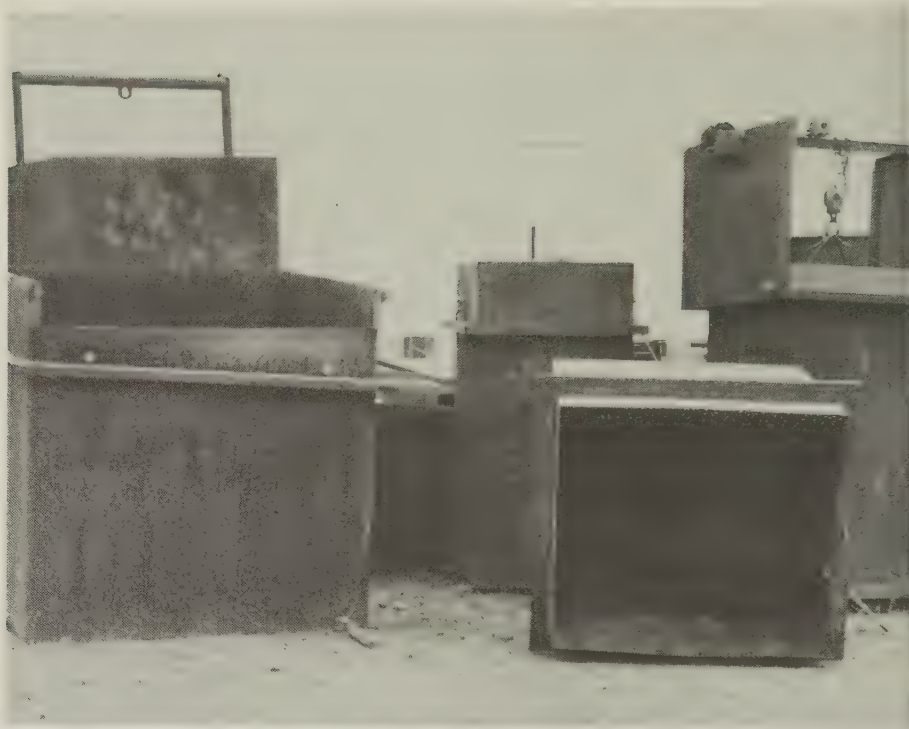


FIGURE 9. Dungeness crab live-tanks. Photo by W. A. Dahlstrom.

cork line and lead line. The middle web or net was constructed of fine mesh, loosely hung, and the guard net on either side was of larger mesh, tautly hung. The mesh of the outside guard nets was usually about three times as large as the mesh of the inner net.

The principle on which the trammel net works is that a fish or crab, upon encountering the net from either side, passes through the taut large mesh, striking the finer and looser inside mesh through which it cannot pass but which is pushed ahead through one of the large meshes on the opposite side, thus, forming a pocket in which the fish is trapped. These nets varied from 20 to 40 fm in length and 2 to $3\frac{1}{4}$ fm in depth. A series of nets was fished as a unit.

The use of trammel nets was prohibited during the years 1911 and 1912. In 1913, the law was rescinded and crab fishing became commercially important in Monterey Bay. Good fishing continued in 1914 with this gear accounting for the bulk of the catch. In 1915, trammel nets were again declared illegal for the Monterey area. It was found that sizable amounts of fish were destroyed by hagfish and large numbers of female and undersized male crabs also were destroyed while attempting to remove them from the nets.

From 1915 until at least the late 1930's, gill nets (a single wall of webbing for catching fish) accounted for most of the Monterey Bay crab catch. According to Phillips (1935), gill nets used in the crab fishery followed a fairly standard pattern. Mesh size of the different nets varied from $8\frac{1}{2}$ to 11 inches, stretched

web measure. The nets were made up into sections, each measuring about 180 ft long and about 9 to 12 ft deep. The upper rope or cork line was threaded with 3-inch corks spaced about a foot apart, and the lower rope or lead line was threaded with 2-oz leads spaced about 6 inches apart. Usually about 10 sections of gill net were tied together, cork line to cork line and lead line to lead line, to form one fishing unit. A 15-lb dory anchor at each end secured the string of nets. Gill nets were usually operated by two fishermen per boat, although sometimes one worked alone.

The task of pulling the nets and extracting live, struggling crabs was often long and tedious. After the nets were pulled aboard, the crabs were removed on the way back to port. If the catch was large, the removal continued for some time after returning to port. Nets were taken ashore about once per week for repair and tanning.

Crab hoopnets were tried in Monterey Bay but were not widely or successfully used according to local fishermen. They indicated that in certain parts of Monterey Bay the nets sank in the soft mud, hiding the bait from the crabs, or that hagfish would consume the bait before it could entice crabs. Since the late 1940's, crab traps have been used exclusively in this area.

The crab fishery in the Morro Bay-Avila area developed after World War II. Although the landings were relatively low, they reached 433,706 lb for the 1950-51 season and averaged 250,510 lb from the 1955-56 season through the 1959-60 season (Figure 2). Since then, the landings have fluctuated at much lower levels.

Both Monterey Bay and Morro Bay-Avila areas are near the southern limit of the Dungeness crab's range and the potential for substantial landings has never appeared to be as great as for more northern areas. Lack of effort may contribute to low landings in these areas; however, the major factor appears to be low abundance of the resource which is probably limited by environmental conditions.

Vessels trawling for a variety of fishes in northern and central California often take Dungeness crabs incidentally in the catch. This has never amounted to a large percentage of total crab landings, but individual catches of crabs, at times, may be considerable. In 1947, legislation was enacted which prohibits the possession of more than 500 lb of Dungeness crabs on a trawler.

Beginning with the 1956-57 season, at least one 4-inch rigid circular escape port was required on each crab trap to allow sublegal-sized males and most females to escape. The lowest portion of the opening had to be no less than 5 inches from the top of the trap. In 1968, this law was amended to require that escape openings be constructed on the top or side of the traps. If side openings are used, at least one-half of the opening must be in the upper half of the trap. In 1969, the law was changed to require at least two 4-inch rigid circular openings in each trap. In 1974, the escape opening size was changed to 4¼ inches for all traps constructed after January 1, 1975. Since 1978, all traps must have 4¼-inch escape openings.

In 1959, a law was enacted which allowed crab fishermen to have 1% of a load less than the 7-inch minimum size but none less than 6 inches in breadth. In 1965, the minimum size was changed from 7 inches measured straight across the back from point to point (tip to tip of 10th lateral spines) to 6¼ inches straight across the back from edge to edge of the shell directly in front of the

10th spines. This change was made because it is an easier method of measurement; however, because the spines are not included, the actual minimum legal size of crabs was not changed appreciably. The 1% tolerance limit also was amended to read that "not more than 1% in number of any load or lot of crabs may be less than $6\frac{1}{4}$ inches, but not less than $5\frac{3}{4}$ inches in breadth."

In 1933, the Eel River and its tributaries were closed to commercial fishing. In 1941, this prohibition was amended to include the Pacific Ocean within a radius of 1 mile from the mouth of the Eel River, Humboldt Bay and the Pacific Ocean within 1 mile from the entrance to the Bay, Trinidad Bay, and Bodega Lagoon. These areas presently (1983) remain closed to commercial crabbing.

THE DUNGENESS CRAB SPORT FISHERY

Sport fishing for crabs on the west coast has probably occurred from the early days of settlement by the pioneers. Total annual sport landings of Dungeness crabs in California are not known but are believed to be only a small fraction of the commercial catch.

Various laws have regulated this fishery over the years. The following were in effect in the "1983 California Sport Fishing Regulations":

Crabs may be taken by hand, baited hoopnets or crab traps.

Sport crab traps in central and northern California must have at least two rigid circular escape openings not less than 4 inches in diameter and placed so that the lowest part of each opening is not less than 5 inches from the top of the trap.

The minimum size limit is $6\frac{1}{4}$ inches, the same as for the commercial fishery, except that female crabs of legal size may be taken by sport fishermen.

The daily limit is 10 crabs. Open season in Del Norte, Humboldt, and Mendocino Counties is from December 1 through July 30 and in all other counties, the second Tuesday in November through June 30.

Areas closed to commercial fishing for crabs from northern California to Bodega Lagoon are open to sport fishing for crabs.

No sport fishing for Dungeness crabs is allowed in San Francisco and San Pablo Bays. Concern over excessive sport take of sublegal Dungeness crabs prompted the California Fish and Game Commission in 1978 to close these bays inside the Golden Gate to the sport take of this species.

Most sport crabbing in California is done with baited hoopnets or various types of folding or rigid traps sold at many coastal sporting goods stores and bait shops. Much sport crabbing occurs from piers and jetties and is often done while angling for sport fish. Some sport crabbing also is done from rowboats and small power boats.

The level of activity and success of crab sport fisheries depend first upon accessibility and secondly on the abundance of legal-size crabs. Some sport fishing for Dungeness crabs occurs from most of the ports from which the commercial fisheries operate. The sport fishery for Dungeness crabs in California probably is most active along the northern coast, especially in the Crescent City area.

Sport crab fishermen fishing from the Crescent City dock and from boats inside and outside the harbor were interviewed during 1965–66, 1966–67, and 1967–68 seasons (Gotshall 1978a). Boat fishermen averaged an estimated 766 fishing days per season and their estimated Dungeness crab catch averaged 4,300 per season. Dock fishermen averaged an estimated 433 fishing days and 272 Dungeness crabs per season.

A little farther south in the Eureka area, most crab sport fishing takes place from small boats inside Humboldt Bay. This fishery was sampled from December 1964 through March 1965 (Poole and Gotshall 1965; Gotshall 1978a). An estimated 800 fishing days during this season produced an estimated 400 Dungeness crabs and 2,223 other crabs (approximately 88% red crabs, *C. productus*, and most of the rest rock crabs, *C. antennarius*). Occasionally, slender crabs, *C. gracilis*, and yellow crabs, *C. anthonyi*, are caught in various crabbing areas, although the yellow crab is more likely to be caught with Dungeness crabs in central than in northern California because its major area of abundance is in southern California.

There is some evidence that Dungeness crab sport-fishing success was better in some years subsequent to those sampled (Gotshall 1978a). Nevertheless, the catches of sport fishermen are insignificant when compared to the commercial catch (Figure 2). Thus, there appears to be good potential for an increase in sport fishing for Dungeness crabs in California.

Chapter 2

THE DUNGENESS CRAB RESEARCH PROGRAM: DIRECTION AND ORGANIZATION

by

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INTRODUCTION

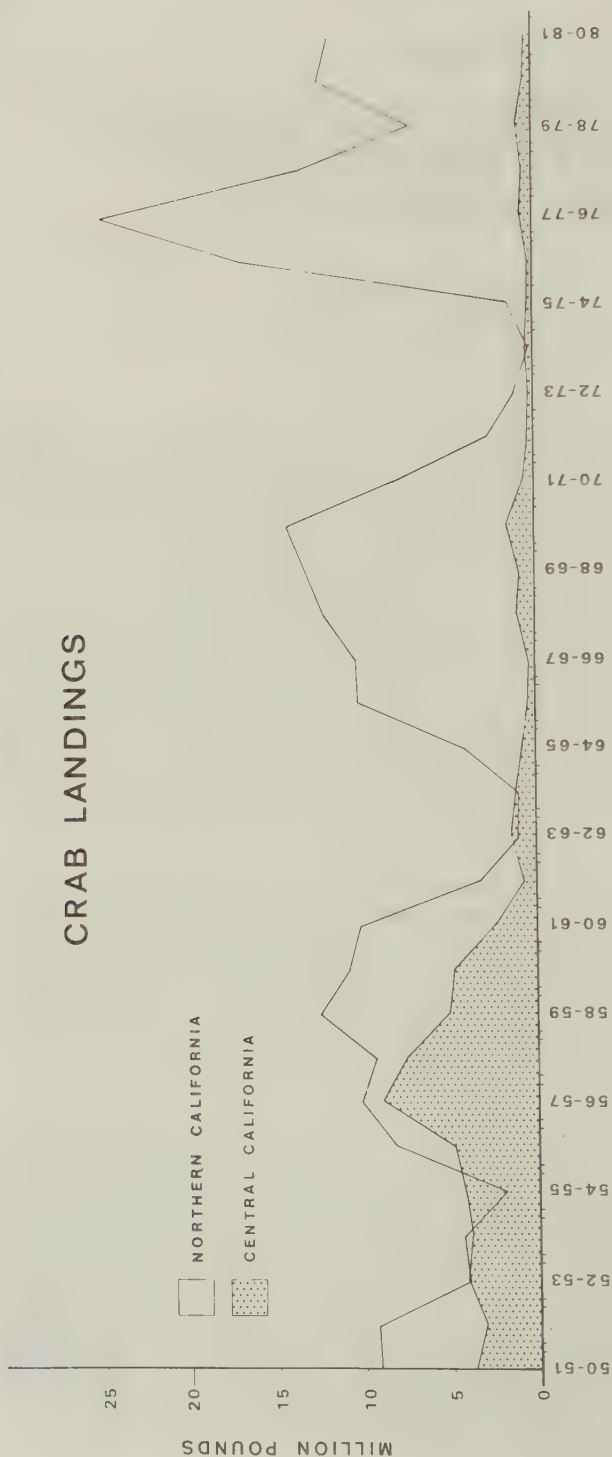
Commercial fishery landings of Dungeness crabs, *Cancer magister*, along the Pacific Coast have fluctuated in a cyclic manner since the 1940's. A 9- to 10-year cycle has been observed. Landings in northern California have continued this cyclic pattern, but those in central California did not rebound in the early 1960's and have continued at unprecedented low levels (Figure 10).

From 1945 to 1960, San Francisco area crab landings averaged 4.8 million lb per season. The landings reached an all time peak of 8.9 million lb during the 1956-57 season and declined at the rate of approximately 2 million lb per season until the 1961-62 season when only 710,350 lb were landed. A slight increase occurred during the 1962-63 and 1963-64 seasons when 1.3 and 1.2 million lb were landed, respectively, and again in 1969-70 with a high of 1.5 million lb. However, the long-term average from 1961 to 1982 was less than 1 million lb per season. The decline of the crab resource in central California is of serious concern because it indicates a long-term trend rather than a short-term fluctuation.

The State Legislature in 1974, by Senate Bill 1606, directed the Department of Fish and Game to conduct an investigation into causes of the long-term decline in the California Dungeness crab fishery. A tax on crab landings was imposed by S.B. 1606; the resulting funds were used to support most of the cost of the investigation. The Dungeness Crab Research Program began in 1974 and was to end September 30, 1979; however, the termination date was extended to June 30, 1980. Annual progress reports and a final comprehensive report were required by the legislation.

There were six progress reports during the Program. Marine Resources Administrative Report 75-8 (Orcutt et al. 1975a) outlined the central California crab problem; presented the objectives of the new program, research design, and work plans for the study, and detailed the results of some preliminary research activities. Marine Resources Administrative Reports 75-12 (Orcutt et al. 1975a), 76-15 (Orcutt et al. 1976b), 77-21 (Orcutt 1977), 78-16 (Orcutt 1978), and 79-16 (Farley 1979) report the results of work done in 1975, 1976, 1977, 1978, and 1979 (through August 31), respectively. A summary report was submitted to the Legislature in February 1981 (Calif. Dep. Fish and Game 1981a) and published in March 1981 (Calif. Dep. Fish and Game 1981b). The present document, Fish Bulletin 172, is the final comprehensive Program report.

CRAB LANDINGS



SEASON

FIGURE 10. Commercial landings of Dungeness crabs in northern and central California for seasons 1950-51 through 1980-81.

PROGRAM DEVELOPMENT

The objective of the Dungeness Crab Research Program was to determine the factors causing the decline and continued low levels of California's Dungeness crab resource in California and to make management recommendations to protect and increase the resource.

Initially, eight hypotheses were generated to explain the crab's decline.

1. San Francisco Bay is an important nursery area for young crabs; its recruits are necessary for a sustained central California fishery, but natural or man-caused conditions prevent survival of adequate numbers of the young crabs.
2. Nearshore ocean water quality has deteriorated due to man's activities to a level below that necessary to support crabs through critical larval and juvenile stages.
3. Satisfactory recruitment levels have been prohibited by effects of natural oceanographic conditions such as temperature, salinity, currents, etc., on larvae and juvenile crabs.
4. Intensive fishing pressure or pollution has lowered the population below a threshold level where natural reproduction is not sufficient to rebuild the resource.
5. Predation and cannibalism keep the crab population at low levels.
6. Crab production is kept low by a lowered food supply.
7. Intensive sportfishing on undersized crabs in San Francisco Bay is a factor affecting recruitment to the commercial fishery.
8. The crab population has been decreased by parasites or disease.

The hypotheses considered to be most applicable to the problem were no. 1, 2, and 3. These hypotheses suggest that larval and juvenile forms occurring in bays and nearshore ocean waters are critical stages, and that the most plausible causes of low survival should be sought in effects of natural and man-caused environmental conditions on these stages. The major effort of the research program was directed toward these three hypotheses, although some effort was devoted to the others. The hypothesis concerning fishing of undersized crabs in San Francisco Bay was not tested due to manpower limitations, but Dungeness crab sportfishing was made illegal in the Bay in 1978.

The research program was divided into two separate, though related, projects: (1) Crab Critical Stage Project, and (2) Crab Environment Project. Crab critical stage studies were directed primarily at determining the occurrence and distribution of early life history stages in the marine environment and associated environmental parameters. Environment project studies were aimed at uncovering any relationships between historic oceanographic conditions and (or) man-caused changes in the environment and fluctuations in crab abundance. Concurrently with the projects' studies, experiments were undertaken by the Department's Marine Culture Laboratory (MCL) to raise test animals for special studies and to develop mass culture techniques for Dungeness crab larvae.

ORGANIZATION OF REPORT

The following 20 chapters describe the Dungeness Crab Research Program's studies in detail. Reports on studies by the Crab Critical Stage Project precede those of the Crab Environment Project. These are followed by chapters describ-

ing MCL studies. The final chapter summarizes the life history of Dungeness crabs in central California; presents the major findings related to the decline and continued low levels of the crab population; offers management options to benefit the crab resource and fishery; and suggests some additional research needs.

Chapter 3

DUNGENESS CRAB CRITICAL STAGE STUDIES, AN INTRODUCTION

by

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INTRODUCTION

The primary objective of this project was to determine if there are any stages in the life history of the Dungeness crab, *Cancer magister*, critical to maintaining central California crab stocks at levels experienced prior to the 1960–61 season. As a result of our review of many studies on adult Dungeness crabs and our assessment of the impact of the commercial fishery, we concluded that any such critical stages probably lie within the crab's larval or juvenile development periods, and that we should concentrate our research efforts there. We sought to determine the extent to which oceanographic factors currently influence life history stages and in this context interfaced with the Dungeness Crab Environment Project.

During initial stages of the project's development, we compiled and reviewed available information on Dungeness crab life history. Information concerning larval and juvenile crabs in central California and some aspects of adult crab biology was scarce, and as a result we planned investigations of the following subjects:

1. Stock identification
2. Oceanographic factors associated with various life history stages
3. Distribution and relative abundance of Dungeness crab larvae and associated zooplankters
4. Distribution, relative abundance, growth rates, and food habits of juvenile Dungeness crabs, and the importance of San Francisco Bay as a nursery ground
5. Predators and their effects on Dungeness crabs

Studies were designed to provide information necessary to satisfy our primary objective.

STUDY AREAS

The principal study areas were the Gulf of the Farallones (Figure 11) and the San Francisco-San Pablo-Suisun Bay complex (Figure 12). These two areas are mentioned so frequently in this and succeeding chapters that the authors often refer to them as "Gulf" or "Bay". Occasionally we use the term "ocean" intending to expand our reference beyond, but not necessarily excluding the Gulf, or limit ourselves to specific portions of the study areas, e.g. "north San Francisco Bay" or "Drakes Bay".

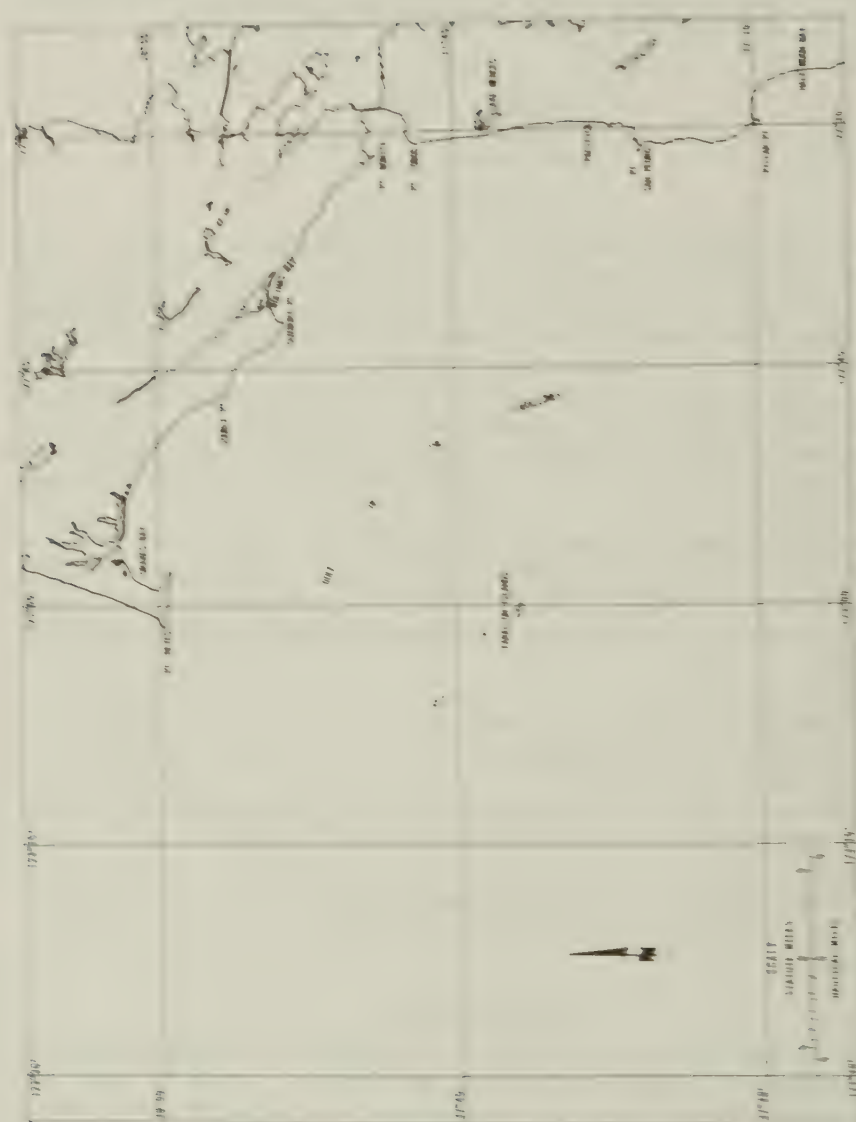


FIGURE 34. Gulf of the Farallones.



FIGURE 13. Station grid for Bay study area.

We divided the two principal study areas into blocks (stations), one minute longitude by one minute latitude, and numbered them consecutively (Figures 13 and 14). Station locations offshore and to the north of the principal study area were assigned numbers after occupation and are not necessarily in sequence. To compare our data with those of other studies, we used location coordinates of all ocean stations sampled (Appendix II).

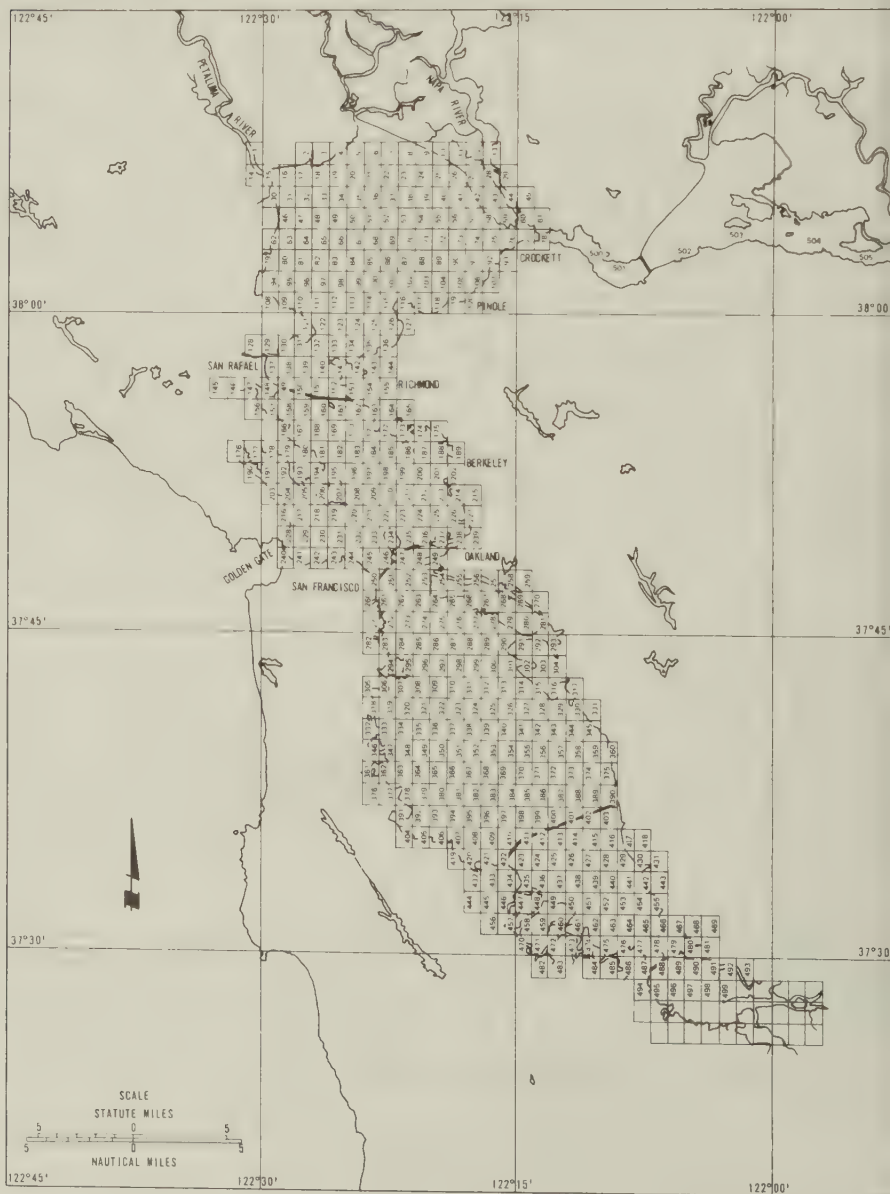




FIGURE 14. Frequently occupied stations along transects in the Gulf of the Farallones.

The principal study areas were sampled from 1975 through 1980. Ocean areas north of the Gulf were sampled from 1977 to 1979. Plankton sampling transects off Eureka (Figure 15) were sampled as frequently as possible during the crab larval period to compare distribution and abundance between northern and central California. In spring of 1979, ocean waters between the Gulf and Cape Mendocino were sampled extensively to investigate distribution and abundance of late Dungeness crab larval stages (Figures 16 and 17).

FIELD OPERATIONS

Project personnel expended considerable time and effort sampling in the field. Cruises from late December to early February were designed to collect early Dungeness crab zoeal stages and oceanographic data associated with them. Similarly, March through April cruises concentrated on late zoeal stages and megalopae, while those from May to July focused on early post-larval instar crabs. Cruises were conducted in autumn to assess abundance of current year-class crabs. Stomachs of demersal and pelagic fishes were collected March–June and September–October to assess the impact of predation. Distribution, growth, and food habits of juvenile crabs in the Bay were investigated on cruises from October through March and by year-round ringnet sampling.

Cruises were the project's major field effort; 61 were conducted totaling 335 days at sea (Appendix III). Duration of these cruises ranged from 1 to 16 days. Generally two biologists were needed to conduct sampling operations at sea. A

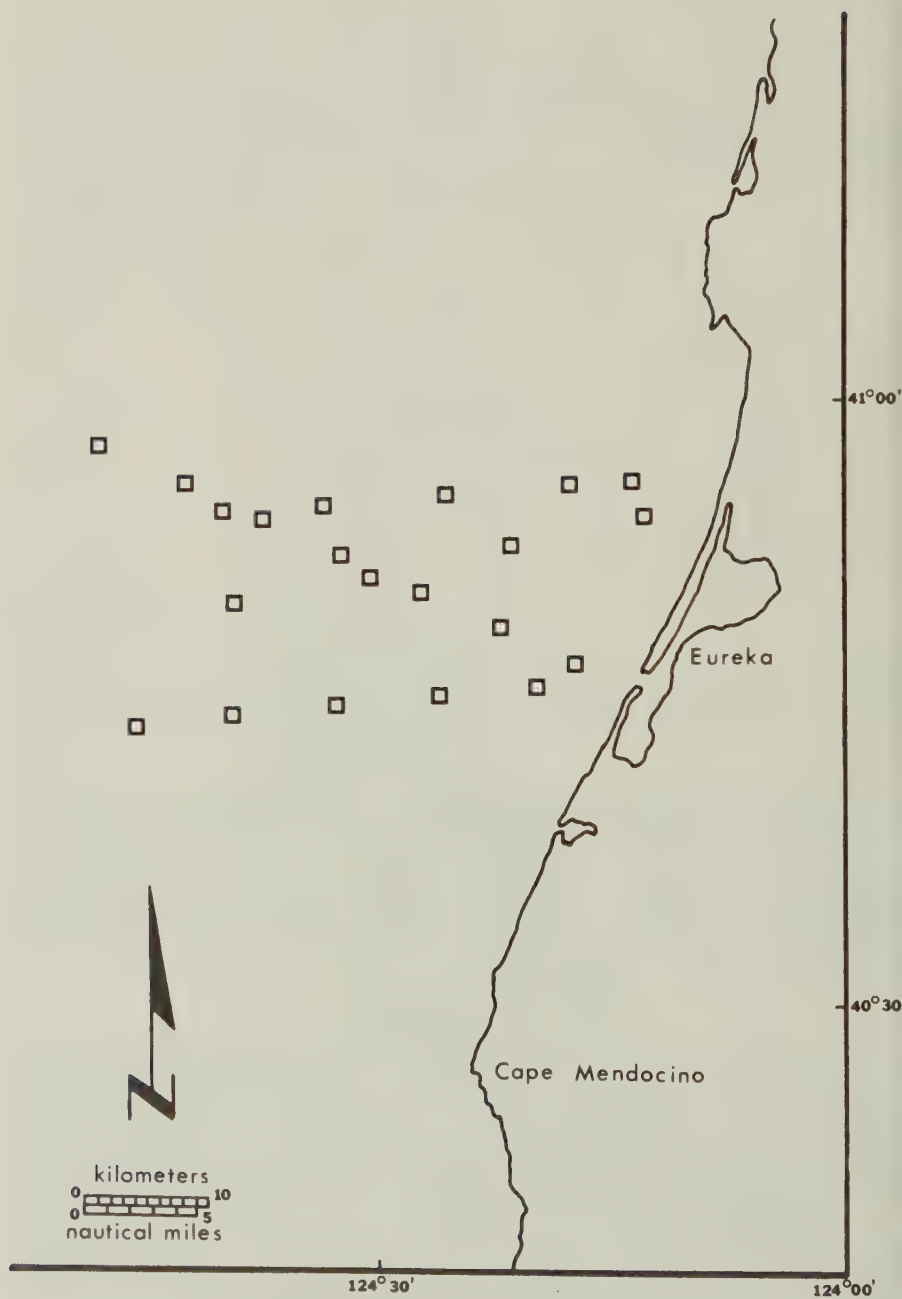


FIGURE 15. Plankton sampling stations off Eureka.

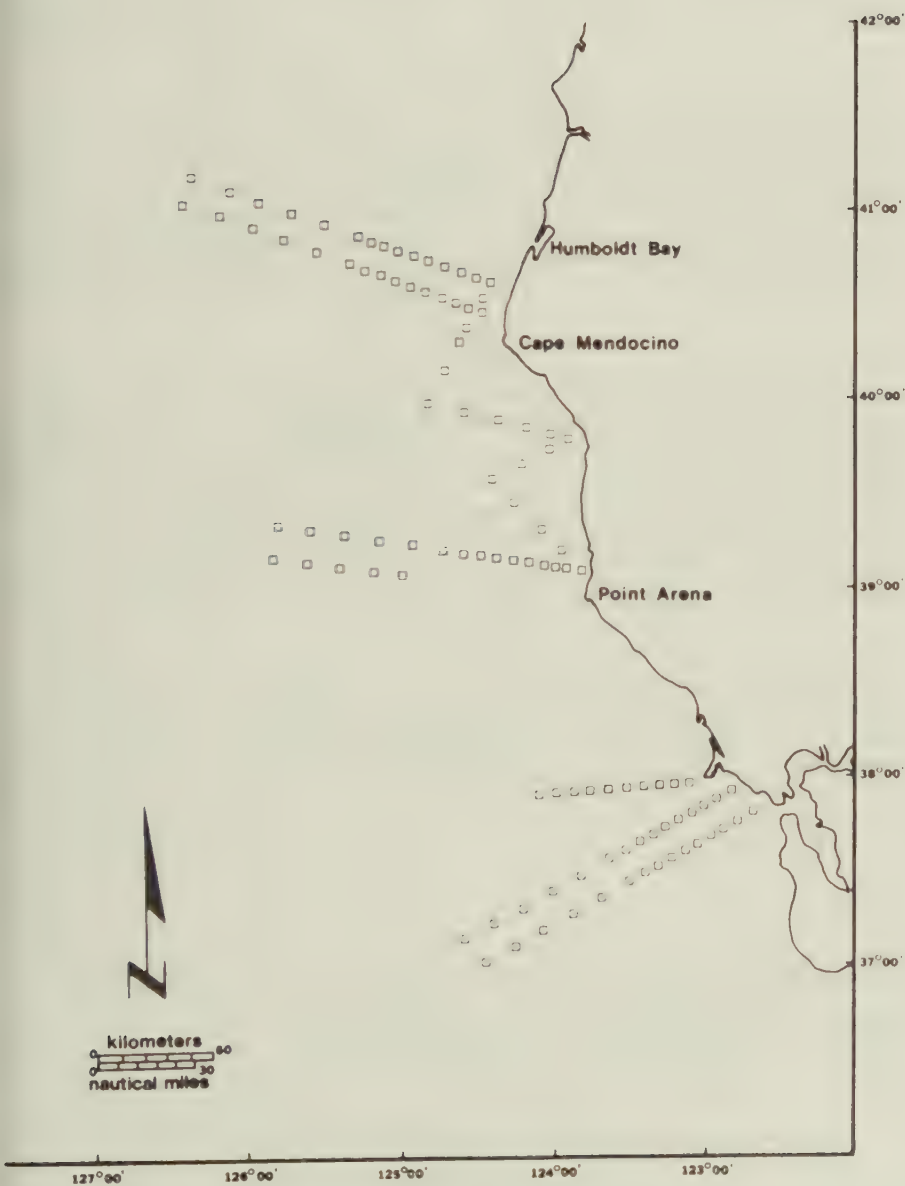


FIGURE 16. Plankton sampling stations, Cruise 79202 (Appendix III).

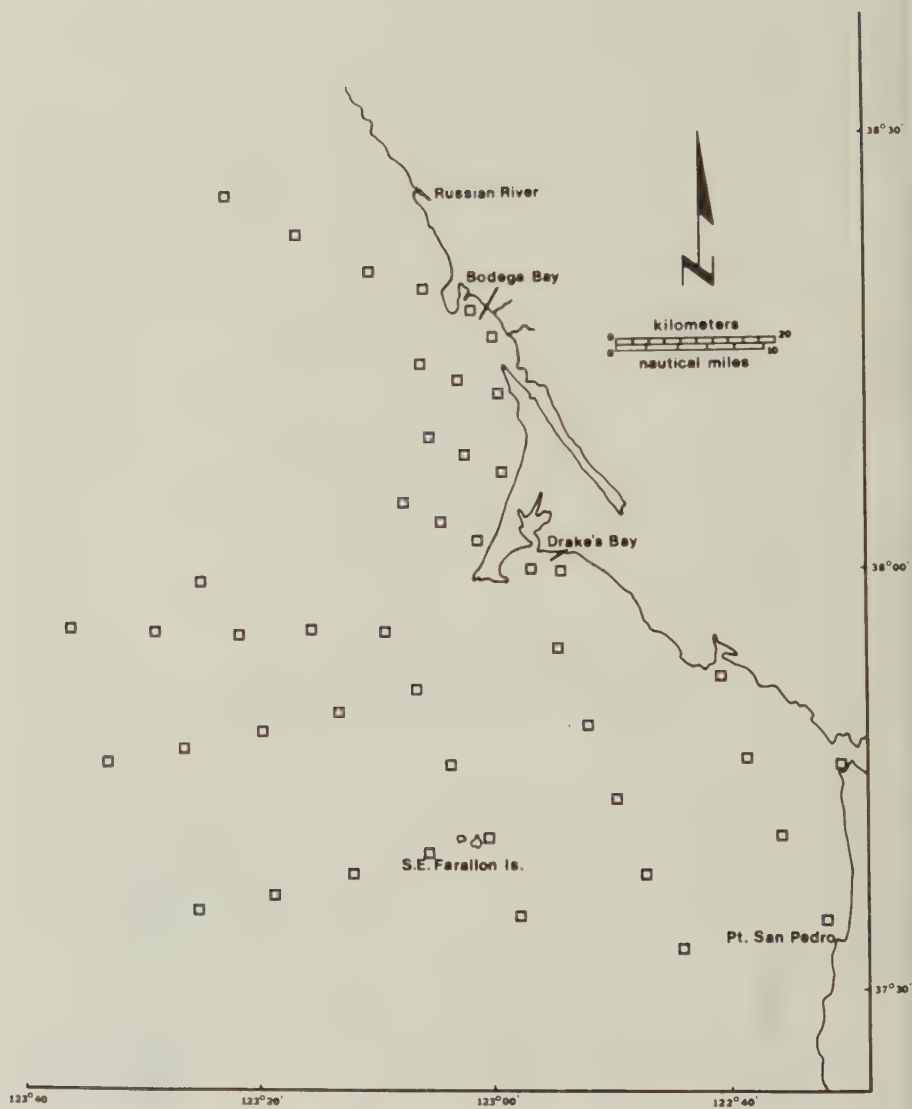


FIGURE 17. Sampling stations, Cruise 79503 (Appendix III).

variety of vessels was employed in field operations, these included: (i) Department research vessels KELP BASS, ALASKA, N. B. SCOFIELD, STRIPER II, and CRAGO; (ii) Department patrol boats BLUEFIN, BONITO, and TUNA; and (iii) charter vessels LITTLE BEAR, OCONOSTOTA, MONICA, NORINE, SANDY B., and CAYUSE. Approximately 200 days were spent ringnetting from piers, jetties, and boat docks.

LABORATORY OPERATIONS

Most of the samples collected in the field were returned to the Marine Resources Laboratory at Menlo Park. Approximately 1800 plankton samples and 2800 fish stomachs were analyzed there. Specimens taken for tissue electrophoresis or for reproductive studies and toxicant bioassays by the Crab Environment Project were examined elsewhere. Analyses were conducted primarily by project biologists, although a small percentage of the non-brachyuran plankton identification was done on contract.

DATA SYSTEM

Data collected in the field and laboratory were recorded on forms designed to facilitate keypunching. Keypunching was provided by the Department's Biostatistics Section at Long Beach or by contract to an outside service. Key punched data were entered into NOMAD, a data base management system, which offers a high degree of flexibility in retrieving data for analysis. Analytical programs came from a variety of sources and are discussed where applicable. Operation of the data system during input, retrieval, and statistical analysis was provided by the Menlo Park Biometrics Unit of the Department's Planning Branch.

PRESENTATION

The following nine chapters detail the methods, results, and conclusions of Dungeness Crab Critical Stage Project studies. Although all project members participated to some degree in each phase of the research, chapter authors were selected on the basis of their contribution to the analysis of the subject matter presented.

Chapter 4

STOCK IDENTIFICATION STUDIES ON THE DUNGENESS CRAB, *CANCER MAGISTER*

by

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And

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INTRODUCTION

California has five commercial Dungeness crab fishing areas, (i) Eureka-Crescent City, (ii) Ft. Bragg, (iii) San Francisco, (iv) Monterey Bay, and (v) Morro Bay-Avila (Figure 18). Other major Pacific coast fishing areas occur from the California-Oregon border to Newport, Oregon (contiguous with Eureka-Crescent City) and from Cascade Head, Oregon north to Destruction Island, Washington (Pacific Fishery Management Council 1979), and in British Columbia and Alaska. California manages its Dungeness crab stocks as two separate units (northern and central California) and differences in fishing seasons are based on environmentally induced differences in crab condition.

Various mark and recapture studies in California (Jow 1960 and 1965; Gotshall 1978b), Oregon (Snow and Wagner 1965), Washington (Cleaver 1949), and British Columbia (Butler 1951 and 1957) show that adult crabs are capable of moving substantial distances up to approximately 100 miles (185 km) along the coast, although north-south movements of a significant nature are not routine. If considering only the intermingling of reproductively active adults, data from these studies suggest that separate subpopulations could exist. Mixing of adults, however, is not the only mechanism by which physically separated stock units can remain within a genetically singular population. In central California, Dungeness crab larvae have a pelagic phase approximately 105 to 125 days (Reilly, Chapter 6). With major currents off California flowing at speeds of 8 to 20 km per day (Reid and Schwartzlose 1962; Schwartzlose and Reid 1972), movement of larvae from one fishing area to another is a distinct possibility. Observations on the morphological features of crabs caught coast-wide suggest that crabs from different fishing areas are genetically similar; although it has been reported that the length-width ratio of crabs caught in the area of Destruction Island, Washington differs significantly from that of crabs from other areas (Pacific Fishery Management Council 1979).

We used electrophoretic techniques to investigate the possibility of genetic and geographic variation in Dungeness crab stocks. The principal objective of this survey was to determine if this species is a single interbreeding unit or, alternatively, is subdivided into partially or completely isolated breeding units.

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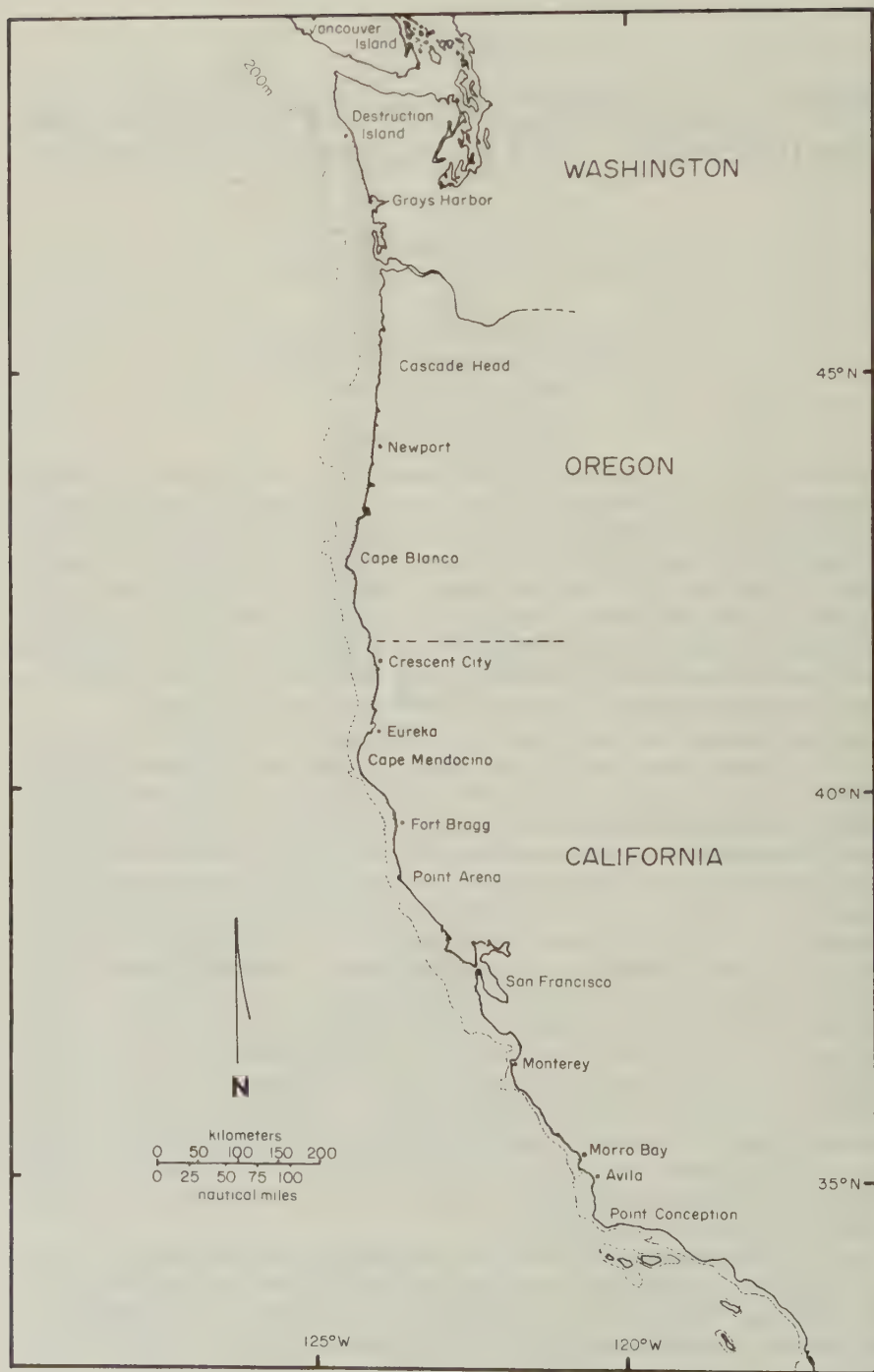


FIGURE 18. Commercial fishing areas for Dungeness crabs off Washington, Oregon, and California. Illustration from Pacific Fishery Management Council (1979)

The Department of Fish and Game's expertise and equipment were too limited for this type of investigation; therefore the study was contracted to the University of California, San Diego. The senior author, a faculty member of U.C. San Diego's Biology Department, was the principal investigator on this study. Laboratory methodology, results, and conclusions in this paper are drawn from two reports submitted to the Department by Soulé. Phase I abstracts the initial report, Phase II the final report. For reasons which will become clear by the end of this chapter, we have omitted much of the technical detail presented in the reports.

PHASE I

Samples of 30 to 35 adult male and female crabs (~135 mm carapace width) were procured from nine localities along the Pacific Coast, five in California and one each in Oregon, Washington, British Columbia, and Alaska. Crabs were frozen and shipped promptly to San Diego.

Processing began with thawing the entire crab until internal tissues could be differentiated. The separate tissues then were homogenized, centrifuged, and refrozen in vials. Various tissues and buffer systems were surveyed to obtain the best combination for reliable "readings" of the stained gels. Four tissues (heart, leg muscle, hepatopancreas, and gonad) and five buffer systems were employed.

Twenty-five gene loci were surveyed and three appeared to show electrophoretic variation. Variation at one of these, the phosphoglucose isomerase locus, was limited to one individual. Two esterase loci appeared to be polymorphic, but one was not readable. The one remaining esterase locus, from both heart and hepatopancreas tissue, appeared to have both fast (F) and slow (S) alleles but showed an absence of a consistent latitudinal cline in frequencies and of geographic variation.

We concluded that the Dungeness crab has very low levels of electrophoretic variation and that uniformity of esterase allele frequencies over the Dungeness crab's range is probably not an accident of sampling nor attributable to homogeneous natural selection. The kind of pattern observed for this esterase has been observed only in species with excellent dispersal mechanisms. These data, therefore, indicated that gene flow in *Cancer magister* is sufficient to prevent local differentiation of populations.

Because of the large number of areas surveyed (nine), the number of crabs per locality was kept necessarily small. Subsequently, we proposed a second study which would survey large numbers of crabs from the two localities of most interest to us, San Francisco and Eureka. Using larger samples, we hoped to establish statistically whether these two stocks were genetically indistinguishable as previously suggested. Phase II reports the results of that study.

PHASE II

Juvenile crabs from San Pablo Bay (Figure 12), a major source of recruits to the San Francisco area fishery, and Humboldt Bay (Figure 16), a minor source of recruits to the Eureka area fishery, were collected for the study. Approximately 800 crabs from each area were provided for analysis. This sample size would permit an estimate of allele frequencies at the esterase locus within about 5% of their parametric values. Laboratory methodologies were to be similar to those developed during Phase I.

After surveying hepatopancreas tissues from more than 100 juvenile crabs, it became clear that the esterase genotype frequencies differed significantly from Phase I. Specifically, the SS phenotype, the most frequent in the adults in Phase I, was rare among these juveniles. Nevertheless, in a sample of 172 juveniles from San Pablo Bay, there was a very good fit between the observed and Hardy-Weinberg genotype frequencies.

Following further tests, during which crabs were classified according to the condition of the hepatopancreas, it was evident that the original (Phase I) genetic interpretation was incorrect. Instead of just one locus with two alleles (slow and fast), each crab had two loci, neither of which was polymorphic. Heart tissue had only the slow-moving enzyme, while hepatopancreas tissue had both fast and slow enzymes. The apparent polymorphism was the result of physiological changes (hepatopancreas depletion vs. replenishment) that were associated with the molt cycle.

The conclusion reached after many tests was that depleted hepatopancreases usually had reduced levels of both enzymes. The major depletion of hepatopancreas reserves takes place after a crab molts and the new soft exoskeleton is hardening. In some cases such hepatopancreas tissues produced no detectable staining for the fast moving enzyme. Replenished hepatopancreas tissues (large, yellow) always had the fast enzyme, whereas the slow enzyme was present in some and absent in others.

Finally, it was concluded that the original esterase "polymorphism" was a physiological artifact that mimicked a Mendelian gene. The study, therefore, failed to disclose any genetic markers that would be useful in stock definition and identification.

CONCLUSIONS

Results of these studies indicate that there is little likelihood of finding useful electrophoretic markers in Dungeness crabs, and that this technique offers little promise in differentiating subpopulations of this species. Thus we return to the most parsimonious assumption: an extensive pelagic larval phase, continuously exposed to strong currents, prevents the development of discrete subpopulations in the Dungeness crab.

Chapter 5

OCEAN AND ESTUARINE CONDITIONS DURING DUNGENESS CRAB CRITICAL STAGE LARVAL STUDIES

by

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INTRODUCTION

Larval stages of the Dungeness crab, *Cancer magister*, are planktonic and a knowledge of ocean conditions associated with their occurrence is necessary to understand their complex patterns of movement, dispersal, and settling. This paper describes aspects of the physical environment during the Dungeness crab larval season in California (December to June) from 1975 to 1980.

During these years we studied distribution and abundance of larvae in the Gulf of the Farallones (Figure 11), San Francisco-San Pablo Bay (Figure 12), and, as time permitted, in coastal waters from the Gulf to the vicinity of Eureka in northern California (Figure 18). We routinely measured water temperature and salinity associated with biological sampling.

METHODOLOGY

Our standard sampling routine for most cruises included temperature and salinity measurements of the water column at the surface, 5 m, 15 m, and 25 m, or the bottom at stations less than 25 m. Bottom temperatures and salinities were recorded at stations greater than 25 m during September and December 1978. At times, temperature data were supplemented with entire water column profiles. Temperatures and salinities were measured with a variety of instruments.

In 1975, at all Bay stations and shallow Gulf stations (15-m or less), a Yellow Springs Instruments (YSI) T-S probe was used. At Gulf stations greater than 15 m, an expendable bathythermograph (XBT) system was used for temperature profiles and Van Dorn bottles were used to obtain water samples for salinity determinations.

In 1976, we used an Interocean Conductivity-Salinity-Temperature-Depth (CSTD) probe in conjunction with the XBT at Gulf stations and the CSTD probe alone for Bay work. The CSTD unit was on loan from the National Marine Fisheries Service (NMFS) Tiburon Laboratory.

From 1977 to April 1978, the CSTD unit was used exclusively until loss of the probe component prompted a return to the XBT, Van Dorn bottles, and YSI probe; these were used until June 1978. During this 2-month period, we also measured surface temperatures with a hand-held thermometer and salinities of water samples were determined with an induction salinometer by the United States Geological Survey (USGS) at their Menlo Park Laboratory.

From June 1978 to April 1980, all ocean and bay temperatures and salinities were measured with a Martek Mark VI Water Quality Analyzer. During the March 1979 cruise on the charter vessel OCONOSTOTA, a surface recording thermometer also operated continuously.

For all of our shore-based crab sampling, the YSI T-S probe was used exclusively except for several months in 1979 in which USGS determined salinities in water samples.

We supplemented and compared our field data with several additional sources of information. Ocean temperature data included sea surface isotherms in 2 F intervals for the northeastern Pacific, published semi-monthly by the National Oceanic and Atmospheric Administration (NOAA) and sea surface temperatures recorded by ships at sea, compiled by NMFS, Pacific Environmental Group, Monterey, CA and available as monthly means in areas bounded by 1° latitude and longitude. Ocean temperature and salinity data were obtained from a 1-year study of the area for a proposed San Francisco Southwest Ocean Outfall (Murphy 1978) and from data collected regularly since 1974 in Trinidad Bay by Humboldt State Marine Laboratory near Eureka.

Current measurements were beyond the scope of our field study, so we relied on both published and unpublished data.

Daily observations of wind direction and velocity at Southeast Farallon Island (Figure 17) from 1976 through 1979 were supplied by the National Climatic Center in Asheville, North Carolina.

SAMPLING RESULTS

Mean surface, 5-m, 15-m, and 25-m temperatures and salinities from Gulf stations during each cruise period were summarized (Tables 3 and 4) to show the range of these oceanographic parameters encountered during 5 years of sampling. Isotherm and isohaline plots for all depths sampled were constructed for each cruise period; a few representative plots are included in the text.

1975 Larval Season

Limited data collected in the Gulf of the Farallones during the spring of 1975 indicate that cold, high-salinity water was present (Tables 3 and 4). We did not observe the extent of estuarine water flow into the Gulf. However, a normal amount of precipitation occurred during the rainy season (November to May). Salinity measurements in San Pablo and northern San Francisco Bays during April and May showed a typical gradient seaward ranging from 11.4 ppt near Crockett to 24.3 ppt near Tiburon (Figure 12). The plume of low-salinity, low density surface water in the Gulf was probably of average size.

1976 Larval Season

Most Gulf temperatures at 15 m during late March (our first major cruise of 1976) ranged between 9 and 11 C (Figure 19), characteristic of upwelled water in central California. An intrusion of colder water (less than 9 C) was apparent in the northern part of the Gulf near Pt. Reyes. Isotherm plots at other depths showed the same intrusion. Most salinity readings in the Gulf were between 30 and 34 ppt, normal for coastal oceanic water in this area. The plume of surface water from the Bay, distinguished by salinities less than 33 ppt, extended only 15 km into the Gulf. The small size of this plume was a result of low freshwater outflow from the Sacramento-San Joaquin Delta during the first of two drought seasons (1975–76, 1976–77). Salinities in the Bay during March were as high as 31.3 ppt near Tiburon and 22.6 ppt near Crockett (Figure 12).

Year	Cruise date	Surface			5-m			15-m			25-m		
		No.	$\bar{x}$	Range	No.	$\bar{x}$	Range	No.	$\bar{x}$	Range	No.	$\bar{x}$	Range
1975	Apr 4-18	7	10.4	9.0-11.7	7	10.0	9.8-10.8	8	9.5	8.9-10.0	5	9.3	8.9-10.0
	May 7-22	9	10.3	8.9-12.2	10	9.7	8.9-12.2	7	9.2	8.9-9.8	-	-	-
	Feb 11	5	11.0	10.1-11.5	5	12.8	11.5-13.5	5	12.3	11.1-13.1	5	12.3	11.1-13.1
	Mar 18-31	33	10.5	8.9-12.3	33	10.2	8.9-12.1	31	10.0	8.7-12.0	18	9.9	8.5-11.8
	Apr 24-May 4	21	10.6	8.6-12.3	21	10.0	8.5-11.6	20	9.1	8.0-11.0	15	8.7	7.6-10.2
1976	May 24-Jun 5	21	10.5	8.9-12.6	20	10.1	8.7-12.3	19	10.0	7.8-11.9	15	9.3	8.5-11.4
	Jun 21-Jul 3	7	12.1	9.5-15.4	1	13.4	-	3	9.4	9.0-10.1	-	-	-
	Sep 27-Oct 8	14	14.3	13.6-15.2	12	14.0	13.4-15.0	3	14.0	13.5-14.6	-	-	-
	Jan 27-Feb 3	39	12.4	10.9-13.5	38	12.4	10.9-13.4	37	12.5	11.0-13.4	32	12.5	11.0-13.2
	Mar 25-26	5	10.4	8.7-11.8	4	10.5	8.7-11.9	3	9.8	8.7-11.8	-	-	-
1977	Apr 6-11	38	9.2	8.3-11.4	38	9.2	8.3-11.3	35	9.0	8.2-11.3	31	8.7	7.9-11.2
	May 9-21	21	11.2	10.1-12.7	21	10.7	9.7-12.4	19	9.7	8.6-12.5	15	9.2	8.2-10.4
	Jun 13-23	23	11.5	9.0-14.8	22	10.9	8.6-13.6	19	9.3	8.3-10.9	16	8.8	8.0-9.4
	Sep 23-Oct 2	22	15.4	14.4-16.7	22	15.0	13.9-16.2	16	14.4	12.4-16.1	5	12.8	11.5-14.0
	Dec 12	8	11.6	11.4-11.7	8	11.5	11.3-11.7	7	11.4	11.0-11.7	6	11.4	11.0-11.7
1978	Jan 6-12	36	13.5	12.6-13.9	36	13.6	12.7-13.9	35	13.6	12.9-13.9	30	13.6	12.9-13.9
	Jan 31	8	12.1	11.9-12.3	-	-	-	-	-	-	-	-	-
	Feb 28	7	13.3	13.1-13.4	7	13.3	13.1-13.4	6	13.2	12.8-13.4	4	13.3	13.2-13.3
	Mar 15-18	35	13.6	12.4-15.0	35	13.2	12.4-14.5	34	12.5	12.0-13.5	30	12.1	11.3-13.1
	Apr 13-24	32	13.7	12.0-15.5	25	12.7	10.6-14.6	21	11.8	10.8-14.3	19	11.0	10.1-11.9
1979	May 27-Jun 3	35	10.3	9.5-12.5	23	10.5	9.4-11.7	23	9.7	8.8-11.1	23	9.2	8.4-10.7
	Sep 16-23	17	14.0	12.4-16.0	15	13.5	11.0-15.9	9	11.7	10.2-13.3	4	11.1	10.1-13.2
	Dec 8-13	26	10.5	10.2-10.9	26	10.5	10.2-10.9	20	10.5	10.3-11.0	11	10.5	10.3-10.7
	Jan 17	7	11.5	10.7-12.1	7	11.6	10.7-12.1	7	11.8	11.2-12.1	5	11.9	11.3-12.1
	Mar 3	8	11.7	11.3-12.5	8	11.3	11.1-11.5	8	11.2	10.8-11.4	6	11.2	10.8-11.4
1980	Mar 14	5	11.9	11.7-12.2	5	11.6	11.3-12.1	5	11.0	10.8-11.4	5	10.8	10.6-10.9
	Mar 20-29	9	11.7	11.2-12.0	9	11.7	11.2-12.0	9	11.4	10.9-11.7	9	11.2	10.4-12.7
	Apr 24-May 6	25	11.8	10.5-12.8	25	11.4	10.0-12.6	22	10.6	9.3-11.9	19	10.0	9.1-11.4
	Dec 27	7	12.1	11.6-12.4	7	12.2	11.8-12.4	7	12.3	12.1-12.4	7	12.3	12.2-12.4
	Jan 7	8	12.3	11.5-13.0	8	12.3	11.7-13.0	8	12.4	11.8-12.9	8	12.4	11.9-12.8
1980	Jan 21	4	12.5	12.4-12.6	4	12.5	12.4-12.6	4	12.6	12.5-12.8	4	12.7	12.5-12.9
	Apr 9	6	11.9	11.6-12.2	6	11.7	11.4-11.9	6	10.1	9.4-10.9	6	9.5	9.3-9.7

TABLE 4. Surface, 5-m, 15-m, and 25-m Salinities (ppt) in the Gulf of the Farallones, 1976-1980.

Year	Cruise date	Surface			5-m			15-m			25-m		
		No.	$\bar{x}$	Range	No.	$\bar{x}$	Range	No.	$\bar{x}$	Range	No.	$\bar{x}$	Range
1976	Mar 18-31	33	33.3	31.5-33.9	33	33.4	31.6-33.9	31	33.5	32.0-34.0	18	33.5	32.2-33.9
	Apr 24-May 4	21	33.6	32.5-34.0	21	33.7	32.6-34.0	20	33.8	32.6-34.0	15	33.9	33.6-34.0
	May 24-Jun 5	21	33.8	32.7-34.2	20	33.8	32.9-34.0	19	33.8	33.0-34.0	15	33.8	33.4-34.0
	Jun 21-Jul 3	7	33.7	33.0-34.0	1	33.3	-	3	33.9	33.9-34.0	-	-	-
	Sep 27-Oct 8	14	32.8	31.9-33.5	12	32.8	32.1-33.5	3	32.6	32.2-33.1	-	-	-
	Jan 27-Feb 3	39	33.3	31.0-33.7	38	33.4	31.9-33.7	37	33.4	31.9-33.7	32	33.5	31.9-33.7
	Mar 25-26	4	33.2	32.6-33.7	4	33.0	32.2-33.7	3	33.2	32.2-33.7	-	-	-
1977	Apr 6-11	38	33.6	32.3-33.9	38	33.6	32.3-34.0	35	33.7	32.3-34.0	31	33.6	32.3-33.9
	May 9-21	21	33.5	32.4-33.9	21	33.5	32.5-33.9	19	33.6	32.4-34.0	15	33.5	32.9-33.9
	Jun 13-23	23	33.5	32.8-33.8	22	33.6	32.9-33.9	19	33.7	33.4-33.9	16	33.6	33.5-33.8
	Sep 23-Oct 2	22	33.3	33.0-33.6	22	33.4	33.0-33.6	16	33.5	33.1-33.6	5	33.5	33.5-33.6
	Dec 12	8	33.3	33.0-33.4	8	33.3	33.0-33.5	7	33.4	33.1-33.5	6	33.4	33.3-33.5
	Jan 6-12	36	33.1	32.0-33.4	36	33.1	32.0-33.5	35	33.2	32.1-33.5	30	33.3	32.4-33.5
	Jan 31	8	28.1	23.4-32.4	-	-	-	-	-	-	-	-	-
1978	Mar 14-18	35	29.8	23.2-33.0	35	31.4	25.6-33.1	34	33.0	30.5-33.3	30	33.1	32.0-33.4
	Jan 31	8	28.1	23.4-32.4	-	-	-	-	-	-	-	-	-
	Mar 14-18	35	29.8	23.2-33.0	35	31.4	25.6-33.1	34	33.0	30.5-33.3	30	33.1	32.0-33.4
	Apr 13-23	25	28.6	24.9-32.4	25	31.3	25.5-32.5	21	32.1	27.1-33.0	19	32.6	32.1-33.0
	May 27-Jun 3	31	33.1	28.2-34.0	-	-	-	-	-	-	-	-	-
	Sep 16-23	17	32.4	31.6-32.9	16	32.6	31.6-33.4	9	33.3	32.4-34.5	-	-	-
	Dec 8-13	26	32.8	31.9-33.4	26	32.9	32.1-33.4	20	33.2	32.3-33.6	11	33.4	32.3-33.6
1979	Jan 17	7	32.0	30.2-33.3	7	32.2	30.6-33.3	7	32.7	31.3-33.3	5	32.9	31.3-33.3
	Mar 3	8	29.6	25.2-33.2	8	31.7	27.7-33.3	8	32.5	28.5-33.4	6	32.8	29.2-33.6
	Mar 14	5	31.5	29.8-32.8	5	31.8	29.9-32.8	5	32.9	32.6-33.1	5	33.1	32.9-33.3
	Mar 20-29	9	32.4	31.5-32.9	9	32.4	31.6-32.9	9	32.7	32.3-32.9	9	32.9	32.7-33.1
	Apr 24-May 6	23	32.6	31.6-33.4	23	32.8	32.0-33.5	21	33.2	32.3-33.7	18	33.4	32.6-34.0
	Dec 27	7	32.4	31.4-32.8	7	32.5	31.8-32.8	7	32.7	32.6-32.8	7	32.7	32.6-32.8
	Jan 7	8	31.6	30.1-32.6	8	31.9	30.6-32.6	8	32.1	30.7-32.7	8	32.2	31.6-32.7
1980	Jan 21	4	30.5	27.8-31.8	4	31.2	28.9-32.4	4	32.6	32.6-32.6	4	32.6	32.6-32.6
	Apr 9	6	30.8	29.7-31.6	6	30.8	29.7-31.6	6	32.5	31.7-32.7	6	32.9	32.8-33.0



FIGURE 19. Temperatures (C) at 15 m in the Gulf of the Farallones, March 18-31, 1976.

By late April surface temperatures in the Gulf were not appreciably different (Table 3) except for a slight increase at southern Gulf stations. Salinities were higher (Table 4) with a corresponding reduction in the plume of estuarine water. Gulf water of salinity less than 33.0 ppt was found only within 2 km west of the Golden Gate Bridge. Cold water temperatures indicative of upwelling continued into late May and early June (Table 3).

During April, May, and June, bottom salinities in the Bay were less than 20 ppt only as far seaward as eastern San Pablo Bay. All surface salinities south of the Richmond-San Rafael Bridge (Figure 12) remained above 28 ppt, while bottom salinities ranged from 29.5 to 32.8 ppt. By June bottom salinity near Crockett had increased to 26.1 ppt. The difference between surface and bottom salinities was greatest in San Pablo Bay, reaching 10 ppt in June. Bay temperature ranges increased from 12.5 to 15.0 C in April to 16.0 to 21.0 C in June.

1977 Larval Season

Our first major cruise of 1977 (late January) encountered an intrusion of relatively warm, well-mixed water in the Gulf, with temperatures between 12.5 and 13.3 C (Figure 20) and salinities between 33.5 and 33.7 ppt. Near Pt. Reyes, a small tongue of colder (~ 12 C) ocean water extended southward toward the Farallon Islands (Figure 20). Estuarine water was evident only within 15 to 20 km west of the Golden Gate Bridge.

By early April upwelling was evident; most temperatures in the Gulf were less than 9.5 C (e.g. Figure 21); interpolation of the 8.5 C isotherm at 15 m (Figure 21) indicates that water in the Gulf was coldest near Pt. Reyes. The surface plume of estuarine water extended about 15 to 20 km into the Gulf.

By May average Gulf surface temperature had increased by 2 C (Table 3), and the extent of estuarine water was confined to within 2 km of the Golden Gate Bridge.

Bay temperatures increased through June to nearly 15 C in central San Francisco Bay, 18 C in San Pablo Bay, and 22 C in southern San Francisco Bay. The salinity gradient remained relatively stable and again reflected drought conditions. Most salinity readings in San Francisco Bay were between 30.8 and 32.6 ppt from January to June. Peak readings in June near Crockett and at Port Chicago (Figure 12) were 28.0 and 22.5 ppt, respectively.

1978 Larval Season

A 1-day cruise on December 12, 1977 encountered well mixed but cool water in the Gulf with mean surface and 25-m temperatures of 11.6 and 11.4 C, respectively (Table 3). Above average rainfall began to cause considerable freshwater runoff into the Bay and influenced the distribution of the salinity gradient there and in the Gulf. In early January relatively warm Davidson Current water was apparent in the Gulf, with mean surface and 25-m temperatures of 13.5 and 13.6 C, respectively (Table 3). Estuarine water was evident between Pt. Reyes and the Golden Gate Bridge within 10 km of shore. On a January 31, 1978 transect from the Golden Gate to the Farallon Islands, Gulf surface salinities ranged from a low of 23.4 ppt to less than 33.0 ppt out to 44 km seaward.

During the March cruise we observed dramatic differences in ocean conditions from the previous two drought years. Surface salinities were less than 33.0 ppt at all but one Gulf station (Figure 22). The majority of estuarine water was located in the northern part of the Gulf with the plume extending 60 to 70 km seaward from the Golden Gate Bridge to near Pt. Reyes, while a small lobe of the plume extended 30 km southwesterly (Figure 22). Throughout this water mass a substantial increase in salinity was observed at approximately 5 m. Most surface temperatures in the Gulf exceeded 13 C.

The April cruise occurred during the transition to the upwelling period. Surface temperatures were still relatively warm, while those at 25 m decreased about 1.0 C from March to April (Table 3). Gulf surface salinities continued to be low (mean = 28.6 ppt); 15-m salinities for all but one station were less than 33.0 ppt, demonstrating vertical mixing of estuarine water. By late May conditions were normal for the upwelling period. Most Gulf surface temperatures were less than 11.5 C, and the plume of estuarine water was evident only within 25 km of the Golden Gate.

In the Bay, salinities decreased significantly during January 1978 (Figure 23). On January 5, 1978, surface and bottom salinities near Crockett were 24.7 and 26.1 ppt, respectively. On January 17, salinities had decreased to 5.1 and 5.7 ppt and, 3 days later, to 1.0 and 3.8 ppt. The range of salinities in south San Francisco Bay was 16.0 to 18.0 ppt. Freshwater runoff reduced salinities throughout the Bay until July. Readings at Port Chicago were 0.0 ppt March–May, 1.0 ppt in June, and 7.5 ppt in July. Typically, higher-salinity water was present in deep channels of central San Francisco Bay. Differences between surface and bottom readings were as great as 23 ppt in March.

1979 Larval Season

December 1978 cruise data showed Gulf waters to be relatively cold and well-mixed, with estuarine water occurring seaward to approximately 20 km.

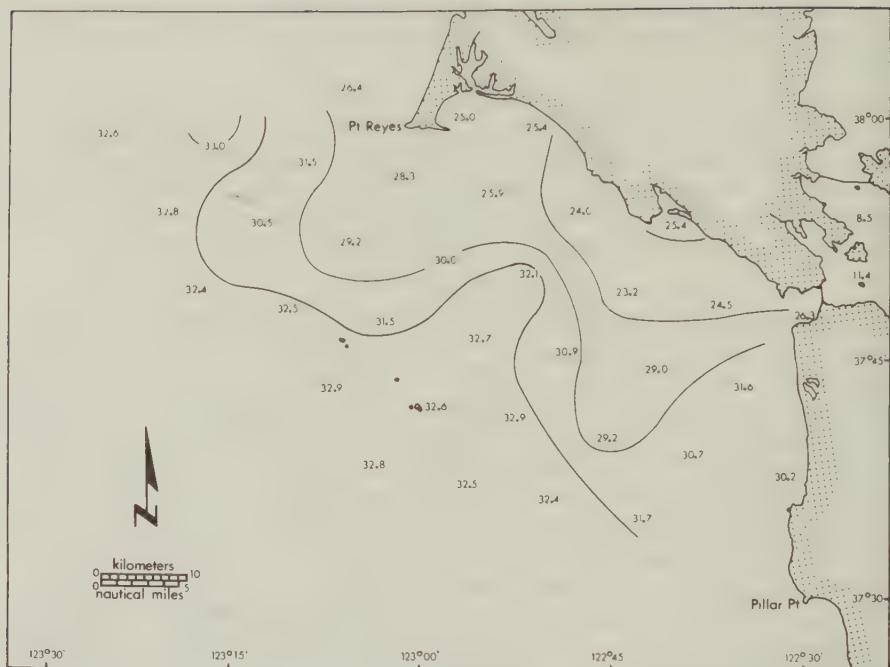


FIGURE 22. Surface salinities (ppt) in the Gulf of the Farallones, March 14–18, 1979.

Gulf temperatures on the January 1979 cruise averaged 11.5 C at the surface and 11.9 C at 25 m, but did not exceed 12.1 C, suggesting a weak Davidson Current. By mid-March, temperatures at 25 m were slightly lower (mean 11.2 C) and surface temperatures slightly higher (mean 11.7 C) (Table 3). Estuarine water had advanced to approximately 30 km seaward.

During an extensive cruise from central to northern California in late March, surface temperatures in and seaward of the Gulf were equal to or greater than 12 C, with the exception of a 70 km wide band of cold water extending into the Gulf near Pt. Reyes. We observed pockets of cold (less than 11 C) upwelled water near the coast from Cape Mendocino to Pt. Arena. However, upwelling was not continuous during this period, and a severe storm with strong southerly winds occurred. With few exceptions, salinity readings were less than 33.0 ppt throughout the cruise.

During the April–May cruise, Gulf temperatures at individual stations were as much as 3.5 C colder at 25 m than at the surface (e.g. 12.6 to 9.1 C). Most 25-m readings less than 10 C were in a 30-km wide band nearshore in the northern area. All temperatures between Bodega Bay and Pt. Reyes were less than 11 C. Surface salinities at stations seaward of the Gulf were similar to those taken in late March, while those in the Gulf and north of Pt. Reyes had increased to as high as 33.4 ppt.

Seasonal rainfall was normal; Bay salinities between December and April ranged from 5.3 to 17.3 ppt near Crockett and from 15.5 to 26.6 ppt at Tiburon.

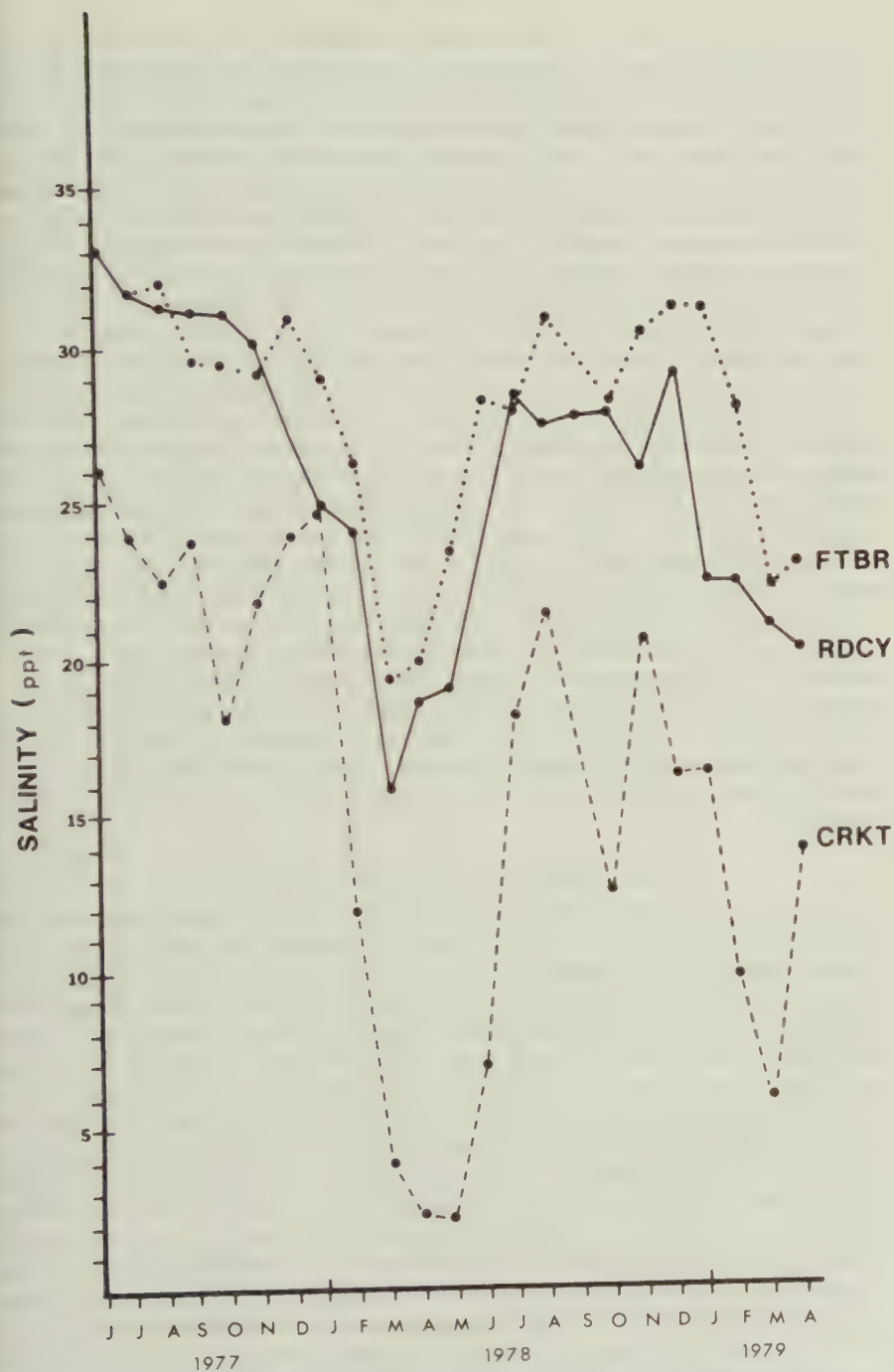


FIGURE 23. Surface salinity (ppt) profiles at Fort Baker, Redwood City, and Crockett in the San Francisco-San Pablo Bay system, June 1977 to April 1979.

1980 Larval Season

During three winter samplings of the transect to the Farallon Islands, we observed higher Gulf temperatures than in the previous winter (Table 3); 13 C surface water occurred in early January at the most seaward stations. Freshwater runoff from abundant rains extended the plume of estuarine water into the Gulf from 15 to 20 km in late December 1979 to approximately 45 km in late January.

NOAA sea-surface charts showed that temperatures in central and northern California remained relatively high until late March when strong northwest winds caused local upwelling nearshore. Temperatures recorded by Humboldt State Marine Laboratory at Trinidad Beach in northern California ranged from 11.7 to 13.2 C during March 1–18 and from 7.9 to 9.1 C during March 24–31. Our April 2–4 cruise in ocean waters near Fort Bragg immediately followed 4 days of gale force northwest winds and surface temperatures averaged 8.8 C. Ten days later, surface temperatures had increased to an average of 11.1 C. Upwelling appeared initially on the April 1–15 NOAA isotherm profile, with surface temperatures less than 11 C nearshore from Half Moon Bay to the Oregon border. Early April temperatures varied at our Gulf and Fort Bragg stations by as much as 2 C between the surface and 25 m (Table 3).

April salinity readings in the northern Gulf continued to reflect above-average rainfall for the 1979–80 season. Surface readings near Drakes Bay were as low as 29.7 ppt and averaged 2 ppt lower than those at 25 m. Surface salinities off Fort Bragg averaged only 0.6 ppt less than those at 25 m. Mean salinities at 25 m were 32.9 ppt in the northern Gulf and 33.0 ppt off Fort Bragg.

Bay salinities in early 1980 followed a pattern similar to 1978 when above-average rainfall caused substantial decreases in January readings. Average surface and bottom salinities at stations north of the Richmond-San Rafael Bridge were 8.3 and 9.6 ppt in January, 7.1 and 8.7 ppt in February, and 4.2 and 4.4 ppt in March.

DISCUSSION AND CONCLUSIONS

Our larval studies were conducted during two major oceanographic periods for central and northern California, generally defined as follows: (i) Davidson Current period, mid-November through February, characterized by relatively warm, northward flowing water; (ii) upwelling period, March through mid-August, with relatively cold, southward flowing California Current water (Bolin and Abbott 1963). A third period, the Oceanic Period, occurs from mid-August to mid-November, with mixed flows and variable water temperatures.

The California Current flows southward and parallel to shore throughout the year. Speed of this current has been estimated at 10 to 20 km/day (Schwartzlose and Reid 1972). Upwelling of cold, high salinity, high density seawater occurs nearshore in the California Current region due to Ekman Transport. Ekman transport is the movement of surface water due to the combined effects of wind stress on the sea surface and the Coriolis force. Northwest winds result in Ekman transport in which surface water is directed offshore and is replaced by colder upwelled water. Between Cape Mendocino and Pt. Conception, Ekman transport is directed offshore for most of the year, although maximum transport occurs between April and August (Bakun et al. 1974). However, net flow during this period is southerly because California Current transport is approximately 14 times greater than Ekman transport (Richard Parrish, National Marine Fisheries

Service, Monterey, pers. commun.). Studies of drift bottles released within 40 km of shore show that surface flow is southward in central California between April and August (Schwartzlose 1963; Hamby 1964). A general circulation pattern compiled from many National Aeronautics and Space Administration (NASA) photographs shows counterclockwise eddies south of Cape Mendocino and Pt. Arena during the upwelling period when the overall flow of the California Current is southward and parallel to the coast (Pirie and Steller 1977).

The northward flowing Davidson Current develops nearshore in a 20 to 90 km wide band during the fall and continuing into the winter, with estimated speeds of 8 to 20 km/day (Reid and Schwartzlose 1962). It has been observed to flow as far north as 50° latitude (Burt and Wyatt 1964). NASA photographs show northerly-moving sediment-laden water nearshore during the Davidson Current period (Pirie and Steller 1977). Near Pt. Arena and Cape Mendocino there is substantial offshore transport of the upper water layers. Between Pt. Arena and Pt. Reyes, meanders develop, but the net nearshore flow is northward toward Pt. Arena. Between Cape Mendocino and Pt. Arena, eddies form and reduce the amount of northerly flow. Hamby (1964) released drift bottles at Bodega Head, California on January 9, 1963; one of these was recovered at Newport, Oregon on March 20, 1963. The relative strengths of the California Current and the Davidson Current may be inversely related (Huang 1972). A stronger Davidson flow may actually be associated with a weaker California Current.

Ocean conditions in the Gulf of the Farallones reflect general coastal patterns but are also affected by estuarine flow from the Sacramento-San Joaquin Delta and the San Francisco Bay system. The effects of precipitation and resultant runoff from the Delta are observed in Bay salinity changes and the extent of the plume of lower-salinity surface water in the Gulf. The Bay is a two-layered system. In central and north Bay, low-salinity, low-density upper layer water moves seaward and is replaced by seawater at depth. In south Bay where runoff is low, bottom water moves northward as it is displaced by a lobe of low-salinity, low-density surface water from central Bay. Bottom water is then entrained in the seawater moving toward the Delta (Conomos et al. 1970).

We have often observed distinct color changes associated with the seaward boundary of the estuarine plume in the Gulf. Estuarine water in the Gulf is usually blue-green and relatively turbid compared with the clear, blue oceanic water. NASA/Landsat photographs of the Gulf in late March 1977 show a counterclockwise gyre of plume water near Pt. Reyes (Pirie and Steller 1977). We did not examine photographs for other years.

A study of seabed (bottom) drifters released in the Gulf during March 1970 indicates that the predominant movement of bottom water was toward the east and into the Bay (Conomos et al. 1970). Movement of drifters into the Bay was most evident within 25 km of the Golden Gate. On the other hand, surface drogues released in the nearshore zone south of the Golden Gate, some in the same location as the previous study, had a 0.02% probability of entering the Bay (Murphy 1978). Schwartzlose (1963) reported surface water movement towards shore from a greater distance seaward in the Gulf during May. The varying strengths of the plume and wind stress (Figure 24), as well as the major ocean currents, undoubtedly affect circulation patterns of Gulf surface water.

Examination of average sea surface temperatures from NOAA data provides a relatively complete description of ocean temperatures for each year of our

study. Surface temperatures from ships at sea and NOAA sea surface isotherm charts support our data which show that Gulf waters during December to June larval seasons (1975=1974-75, etc.) in 1975, 1976, and 1979 were relatively cold compared to 1978 and 1980; in 1977 the Davidson Current period was relatively warm followed by a relatively cold upwelling period.

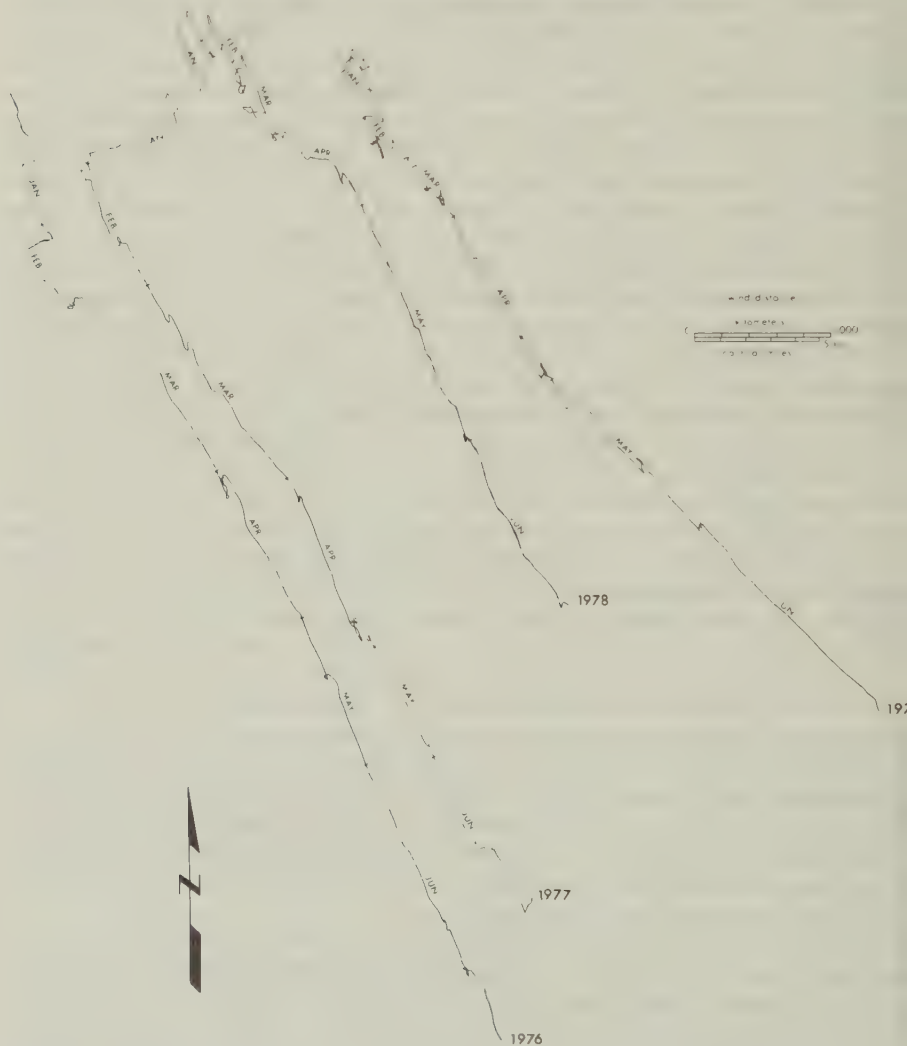


FIGURE 24. Progressive vector diagrams for winds at Southeast Farallon Island, January through June 1976-1979. Daily vectors were computed from mean of two observations, 0620 and 1520 PST.

The presence of 13 C water during January and February was probably the best indicator of the development of a strong Davidson Current in central California; this occurred in 1977, 1978, and 1980. Temperatures reported b

Murphy (1978) for nearshore Gulf waters in January and February 1978 were greater than 13 C. Temperatures in northern California near Eureka showed yearly variations similar to the Gulf, although averaging 1 to 2 C lower during the larval season. Readings at Trinidad Bay by Humboldt State Marine Laboratory exceeded 11 C for the December to February period ending in 1977, 1978, and 1980. 1978 was an anomalous year in which surface temperatures in the Gulf and at Trinidad Head exceeded 13 C and 12 C, respectively, through late April. In March 1978, Trinidad Bay Temperatures reached 13 C.

NOAA isotherm charts demonstrate that upwelling first occurred between Cape Mendocino and the Gulf during April or May in each year of the study. This is substantiated by data which show fairly strong and persistent northwest winds during that period (Figure 24). Our temperature data indicate that local upwelling events occurred in late March each year from 1976 through 1980. April 1977 was the only month in which we found the average surface temperature in the Gulf to be less than 10 C. Wind data (Figure 24) indicate that, compared to other years, strong upwelling also may have occurred in the Gulf in March 1977. In March 1976, April 1977, and March 1979 we observed pockets of cold water extending southward into the Gulf near Pt. Reyes. Although we did not calculate geostrophic flow in the Gulf, these pockets most likely reflect the presence of the California Current nearshore.

Chapter 6

DYNAMICS OF DUNGENESS CRAB, *CANCER MAGISTER*, LARVAE OFF CENTRAL AND NORTHERN CALIFORNIA

by

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INTRODUCTION

The Dungeness crab, *Cancer magister*, passes through five zoeal stages and one megalopal stage after hatching from eggs carried on the abdominal pleopods of the female (Figure 25). A pre-zoeal stage of approximately 10 to 15 min duration has been observed in the laboratory and, although it has not been collected in the field, is considered a normal developmental stage (MacKay 1934; Buchanan and Milleman 1969). The zoeae are entirely planktonic. The megalopa, the final larval stage, is planktonic until settling to the bottom and molting to the first post-larval instar. The larval stages range in length (tip of rostral spine to end of telson) from approximately 2.5 mm for stage I zoeae to 11.0 mm for megalopae (Poole 1966).

Several field studies report on the occurrence of Dungeness crab larvae. Various observations in the Gulf of the Farallones off San Francisco are recorded in California Department of Fish and Game research cruise reports between 1956 and 1970. Dungeness crab larvae were recorded at a Gulf station during a pre-design study on marine waste disposal (Brown and Caldwell 1973). Wickham (1979b) collected megalopae in plankton tows and on the hydroid *Veleva veleva* in ocean waters near Bodega Head, California. Lough (1974 and 1976) found all zoeal stages and megalopae in Oregon waters in 1970 and 1971. Mayer (1973) reported the occurrence of megalopae in Similk Bay, Washington. On the east coast, Sandifer (1973 and 1975), in a study of decapod crustacean larvae in and near Chesapeake Bay, reported on the occurrence of rock crab, *C. irroratus*, larvae and discussed transport and recruitment of larval stocks. Nevertheless, Dungeness crab larval dynamics and life history were not well understood when we began our study.

The purpose of our study was to investigate Dungeness crab larval life history and relate field observations of distribution, relative abundance, and behavior to possible mechanisms associated with the decline and continued low level of the crab resource in central California. Our studies were conducted from 1975 to 1980.

METHODOLOGY

We initiated our larval sampling having limited past experience with methods and equipment necessary to achieve our objective. As a result, we frequently altered procedures during the study after considering factors such as efficient use of vessel time, experimental gear, probable larval stages we would encounter during a cruise, and knowledge gained from previous cruises.



FIGURE 25. Zoel stages I-V and megalopa of the Dungeness crab; A. Zoel stage I, B. Zoel stage II. . . (from Poole 1966).

Field Sampling

In 1975, the majority of our plankton sampling in the Gulf (Figure 11) consisted of horizontal, discrete-depth tows at the surface and at depths of 5, 15, and 25 m (where possible) using a 0.5-m diameter, 0.505-mm mesh plankton net with opening and closing capabilities. Several bottom to surface oblique tows were conducted at shallow stations (less than 15 m) with a 0.5-m, 0.343-mm mesh net. This same net was used for all surface and oblique tows in San Francisco-San Pablo Bay (Figure 12) that year. From December 1975, we routinely included one oblique tow at each plankton station.

A series of 1-day cruises was conducted in the Gulf and the Bay using the 0.343-mm mesh net from December 1975 to March 1976. After these cruises, we discontinued sampling with this mesh size because of problems with clogging during a phytoplankton bloom in the Gulf. The 0.505-mm mesh proved adequate for retaining stage I zoeae. During major cruises in March and April–May 1976, one oblique and four discrete-depth tows were conducted at each Gulf station. For the May–June cruise of that year, plankton sampling at Gulf stations was reduced to surface and oblique tows to allow for trawling operations at a time when we expected to find early post-larval instars.

During a major cruise in January–February 1977, sampling procedures were similar to the previous spring. However, 97 of 137 discrete-depth tows in the Gulf were made with a 12-inch (0.305-m) diameter, 0.505-mm mesh, opening-closing Clarke-Bumpus sampler which was equipped with a flowmeter to measure the volume of water filtered. The small mouth diameter and high flow impedance at normal towing speed (approximately 2 knots) made its use impractical, particularly at offshore stations where brachyuran larval densities were low. This sampler was no longer used after a 3-day cruise in mid-March when we began to use digital flowmeters attached to the 0.5-m opening-closing and other 0.5-m diameter, 0.505-mm mesh nets. Prior to the use of flowmeters, volume of water filtered had been calculated using towing speed of the vessel, duration of tow, and area of the mouth of the net.

In January 1977, we began conducting some plankton tows at night to investigate vertical migration of Dungeness crab larvae. In April 1977, 12 stations were sampled once during the day and once at night to compare day versus night catches of megalopae in surface and oblique tows. All surface and oblique tows were conducted with the 0.5-m, 0.505-mm mesh net during this cruise. For Bay work in May 1977, we attached a 0.5-m diameter, 1.0-mm mesh net to a towing sled (Figure 26) to sample plankton within 1 m of the bottom. This larger mesh size retained all Dungeness crab larval stages except possibly stage I zoeae. However, we used it only when we expected to find late-stage (IV and V) zoeae and megalopae.

Our sampling routine for early-stage zoeae during the January 1978 cruise was similar to previous years, although many oblique and discrete-depth tows in the Gulf were conducted at night to determine vertical distribution of stage I zoeae. We also made replicate tows at three stations to estimate sampling variability of stage I densities. A 1-day, eight-station transect from the Golden Gate to the Farallon Islands was sampled three times from December 1977 to February 1978 during the 1978 larval season. On major cruises in March and April 1978, bottom tows were made with the sled to determine if late-stage zoeae were associated with the ocean bottom. Routine oblique and discrete-depth tows also were conducted during the spring cruises.

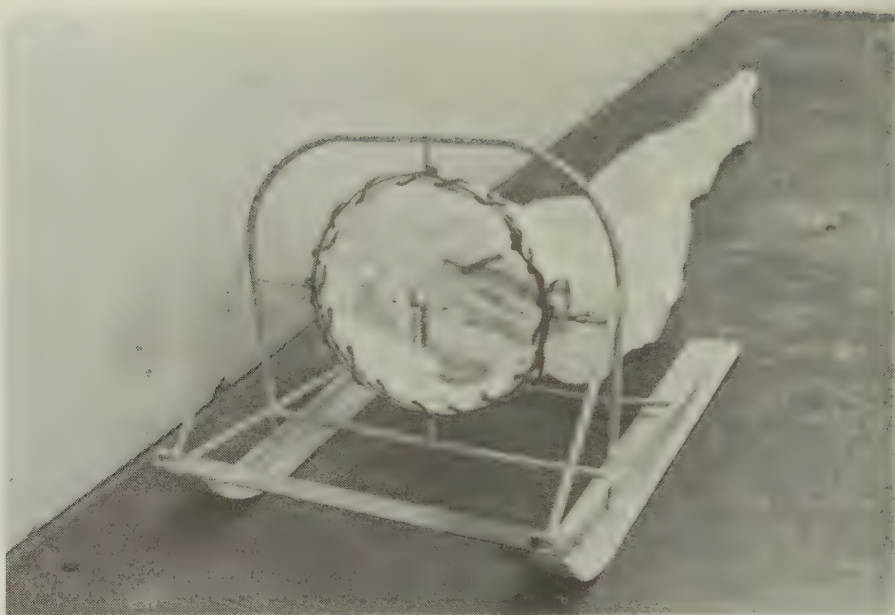


FIGURE 26. Towing sled and net used to sample plankton at ocean bottom. Photo by Paul W. Wild.

We completed three transects to the Farallon Islands between December 1978 and March 1979, the last on a chartered commercial salmon troller. In 1979, we concentrated our efforts on late-stage zoeae and megalopae. During the March 20–29 cruise aboard the R/V OCONOSTOTA, chartered from Moss Landing Marine Laboratories, we extended our sampling out of the principal study area north to Cape Mendocino and to 185 km from shore (Figure 16). We made oblique tows with the 1.0-mm mesh net to 100-m depth or the bottom at shallower stations. Discrete-depth plankton samples were taken at selected stations. The April–May 1979 cruise in the Gulf and Bodega Bay area (Figure 17) consisted of surface and oblique tows with the 1.0-mm mesh net.

As we determined the minor importance of the Bay relative to Dungeness crab larval dynamics, we reduced our effort there. We conducted 65 Bay plankton tows in 1975, 77 in 1976, 50 in 1977, 29 in 1978, 23 in 1979, and 0 in 1980.

Limited sampling during the 1980 larval period began with three transects to the Farallon Islands between late December 1979 and late January 1980, all of these aboard a chartered commercial crab boat. In early April, we chartered a commercial salmon troller from Fort Bragg (Figure 18) and the R/V CAYUSE from Moss Landing Marine Laboratories to obtain additional data on the distribution of megalopae in northern and central California. Surface and oblique tows were conducted with the 1.0-mm mesh net, and discrete-depth tows with the opening-closing net were made in the Bodega Bay area.

We obtained additional data on distribution and abundance of larvae in northern California (Figure 15) by sampling along transects off Eureka in February and April 1977, March 1978, March 1979, and January 1980.

We occasionally used methods other than plankton tows to sample megalopae. In June 1977, April 1978, April–May 1979, and April 1980, we dipnetted *Uca tangeri* from ocean surface waters to examine for presence of megalopae. We also dipnetted megalopae which were attracted to a nightlight suspended over the water from our anchored vessel at various Gulf locations during our April–May 1979 cruise.

All plankton samples were preserved in 10% buffered formalin upon collection. The following data were recorded for each sample: date; cruise, station, and accession numbers; station depth; tow type (horizontal or oblique), time, depth, and duration; and volume of water filtered. We calculated tow depth after measuring wire angle and amount of wire out.

Laboratory Operations

Cruise Samples

Plankton samples were returned from the field to the Menlo Park laboratory where they were inspected and settled volume was measured. We used a Folsom wheel to split samples in which brachyuran densities were high (generally those samples collected in the Bay and at nearshore coastal stations) or those in which the settled volume exceeded 200 ml. A series of 2-ml aliquots, taken with a Stempel pipette, was analyzed if densities remained high after splitting. We examined the entire sample, or all of one of the split portions, with a binocular microscope. Brachyurans were removed, identified to family or, for *Cancer* larvae, to species and stage, and enumerated. Densities of brachyurans (no./m³ of water filtered) were recorded on standardized computer forms which were keypunched and stored. Selected morphological measurements of all *Cancer* larval stages were recorded. Larvae were identified by using published and unpublished manuscripts and samples of larvae cultured at the Department's Marine Culture Laboratory near Monterey.

CalCOFI Samples

CalCOFI (California Cooperative Oceanic Fisheries Investigations) cruises have collected plankton samples off the California and Baja California coasts since 1949. These samples are curated by Scripps Institution of Oceanography, La Jolla, California. We examined samples taken between 1949 and 1975 along transects perpendicular to the coastline between the Oregon border and Pt. Santa Cruz and to approximately 320 km seaward (Figure 27). No samples were collected north of Pt. Santa Cruz in 1955, 1957, 1967, 1970, 1971, 1973, and 1974. Only in 1949, 1950, 1958, and 1960 were samples collected north of Pt. Reyes. We analyzed samples taken from January to early May for presence of brachyuran larvae. The number of samples examined from any one year ranged from 5 to 74. Although spaced widely in distance and time, they provided some historical data on occurrence and distribution of Dungeness crab larvae off California. Data recorded for each sample included the following: date; cruise and station number; station depth and distance from shore; time, depth, and duration of tow; and volume of water filtered. Brachyuran larvae were identified and enumerated by the methods discussed previously.

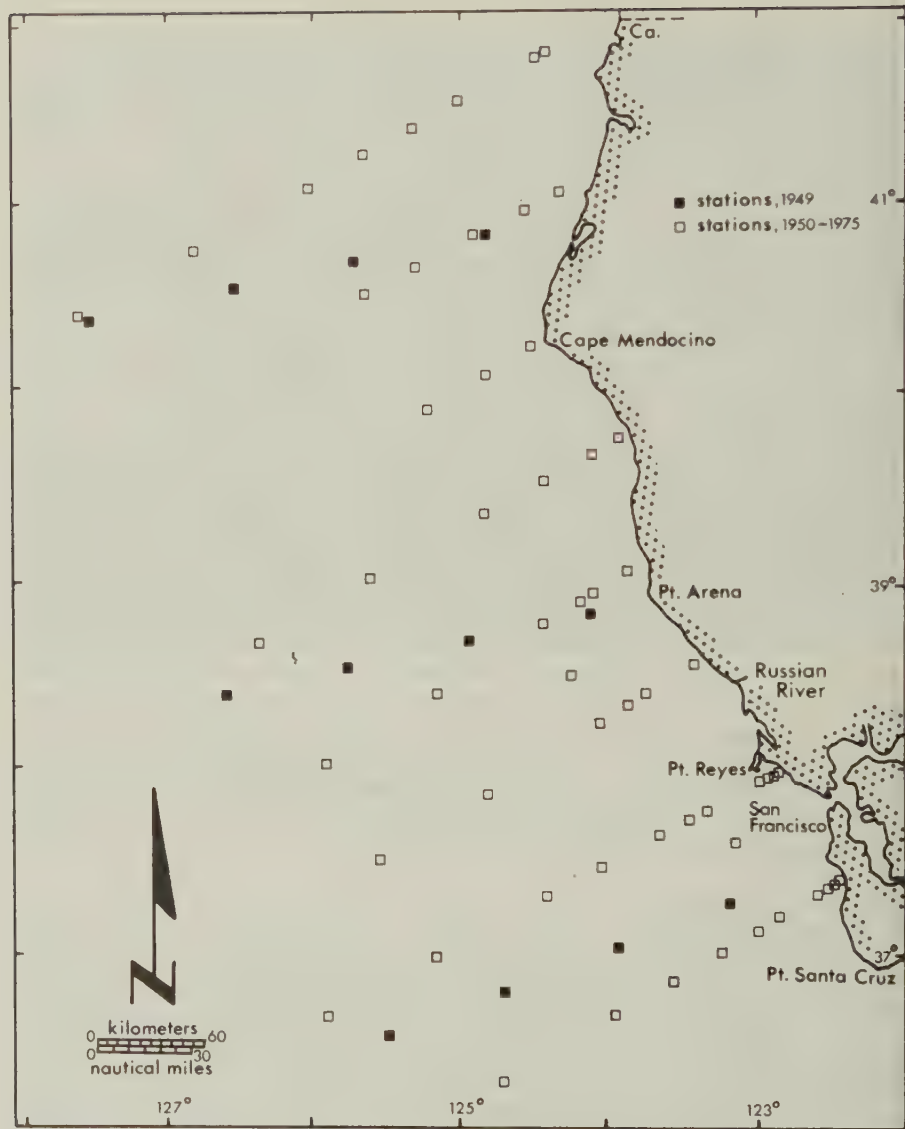


FIGURE 27. Central and northern California CalCOFI stations, 1949-1975.

RESULTS

From April 1975 through April 1980, we collected 1,914 plankton samples. 1,670 were from ocean stations and 244 from Bay stations. Routinely recorded plankton station data are summarized in Appendices IV and V. In addition, we examined 404 CalCOFI samples, all from ocean stations. Our samples yielded 11,560 Dungeness crab larvae and 1,910 were found in CalCOFI samples (Table 5); only two zoeae and 97 megalopae came from Bay stations.

Table 5. Numbers of Dungeness Crab Larvae by Stage Collected from Program and CalCOFI Samples.

<i>Stage</i>	<i>Program samples</i>	<i>CalCOFI samples</i>
Zoea I	8,782	733
Zoea II	426	548
Zoea III	266	270
Zoea IV	153	106
Zoea V	707	110
Megalopa	1,226	143
Total	11,560	1,910

Timing of Larval Occurrences

The initial appearance of Dungeness crab larvae by stage in our studies and CalCOFI samples ranged from mid-December for stage I zoeae to early March for megalopae (Table 6). Mel Willis (Calif. Dep. Fish and Game, unpublished data) found stage I zoeae in the Gulf in late November 1969. We found stage I zoeae at low densities as late as mid-May.

TABLE 6. Range and Earliest Date of First Occurrences of Dungeness Crab Larval Stages in Program and CalCOFI Samples.

<i>Stage</i>	<i>Range of first occurrences</i>	<i>Date of first occurrence</i>
Zoea I	Mid-Dec-early Jan	Dec 12
Zoea II	Early Jan-late Jan	Jan 6
Zoea III	Early Jan-mid-Feb	Jan 6
Zoea IV	Late Jan-late Feb	Jan 23
Zoea V	Mid-Feb-mid-Mar	Feb 15
Megalopa	Early Mar-mid-Apr	Mar 6

We found ovigerous (egg brooding) female Dungeness crabs in the Gulf as early as late September, although most apparently spawn during October and early November; most of the larvae hatch by late January. We estimated time of hatching from changes in density of stage I zoeae and time of first occurrence of stage II zoeae or, as in 1975 and 1977, we inferred it from first occurrences of late-stage zoeae. Onset of hatching was early when Gulf water temperatures during late fall and early winter were warm and later when they were cool. Each year there was apparently one peak hatching period in the Gulf of 1 to 2 weeks duration (Table 7) although a small amount of hatching occurred earlier and (or) extended well into the spring.

The January 6, 1978 appearance of a stage III zoea occurred in the same larval period in which we found stage I zoeae on December 12, 1977 (Table 6). We did not sample between these dates, but some stage II zoeae most likely were present in late December that year.

Based on the first appearance of post-larval crabs each spring in the study area (Tasto, Chapter 9), I estimate the length of the larval period (time for development of individual larvae) in central California to be approximately 105 to 125 days; approximately 80-95 days are required to complete the five zoeal stages and the remaining 25-30 days are spent in the megalopal stage.

TABLE 7. Estimates of Peak Hatching Periods for Dungeness Crabs and Mean December-January Sea Surface Temperatures in the Gulf of the Farallones for Larval Season 1975-1980.

Larval season	Mean surface temp. (C) December-January *	Estimated peak hatching period
1975.....	11.8	Jan 1-10
1976.....	10.6	Jan 11-20
1977.....	12.8	Dec 26, 1976 to Jan 4, 1977
1978.....	13.1	Dec 21-30, 1977
1979.....	11.1	Jan 1-10
1980.....	12.9	Dec 21-30, 1979

* December readings are for the year prior to the assigned date for the Larval season.

Although no CalCOFI samples were collected north of Pt. Reyes in early January, we collected some data to compare relative timing of larval development in central and northern California. In January 1980, we sampled transect 1 day apart in the Gulf and off Eureka. Zoeal stages I and II occurred in both areas in approximately equal proportions. In mid-February 1977, we found stage IV zoeae off Eureka. They occurred in CalCOFI samples from northern California as early as January 24 in 1960, while stage V zoeae and megalopae were present as early as February 15 and March 8, respectively, similar to results from central California.

However, during our late March 1979 cruise, stage III zoeae occurred at densities similar to stage V zoeae in oblique tows off Eureka, but were scarce in central California. Ten days previously, samples off Eureka yielded relatively high densities of stage II and III zoeae during a time when we expected to find primarily late-stage zoeae. Thus, these data indicate that the major hatching period appears to be longer in northern California which would result in a longer larval season for the northern California population as a whole.

Distribution of Larvae in Bay and Gulf

Zoeae

We never found ovigerous female Dungeness crabs in San Francisco Bay east of the Golden Gate Bridge nor any other evidence that the larvae hatch there. In 244 plankton tows in the Bay, the only Dungeness crab zoeae we collected were one stage I and one stage II, both on February 13, 1976 in central San Francisco Bay. Hatching of other *Cancer* larvae does occur in the Bay, and we collected ovigerous females and early-stage zoeae of the red crab, *C. productus*, slender crab, *C. gracilis*, rock crab, *C. antennarius*, and yellow crab, *C. anthonyi* there during our study.

During the 5 years of the study, we found stage I Dungeness crab zoeae at most of our routinely sampled Gulf stations (Figure 28). Relatively high oblique tow densities of stage I zoeae were found at Gulf stations with bottom depths of 30 to 70 m. On 26 occasions, stage I zoeae were collected in these tows at densities greater than 20/100 m³; only one of these occurred at a station not within this depth range. During the January 6-12, 1978 cruise, stage I zoeae were absent at many stations within 5 km of shore and in the outer reaches of the Gulf (Figure 29).



FIGURE 28. Distribution of Dungeness crab stage I and II zoeae in the Gulf of the Farallones, 1975–1980.

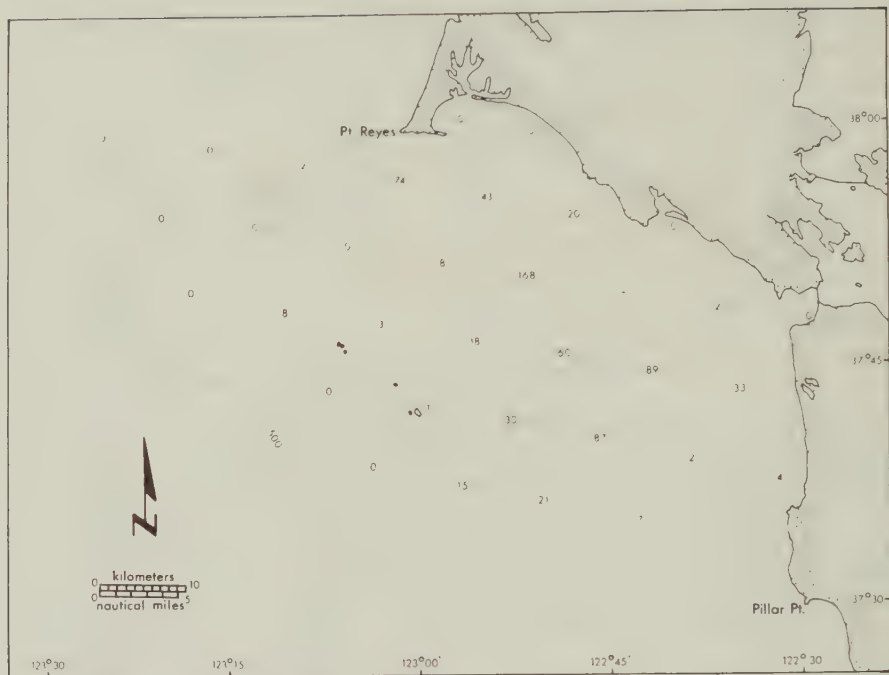


FIGURE 29. Oblique tow densities (number/100 m³) of Dungeness crab stage I zoeae in the Gulf of the Farallones, January 6–12, 1978.

Our data suggest that Dungeness crab larvae occupy a unique niche among larval brachyurans in the Gulf. At most stations greater than 30-m depth, Dungeness crabs were the most common brachyuran stage I zoeae in our January samples, usually occurring at far greater densities than any other species. Occasionally, they co-occurred with stage I *C. productus* and *C. oregonensis*, but these species have a longer hatching season in central California, particularly *C. productus*.

Diel vertical migration of Dungeness crab stage I zoeae was evident in day and night samples collected from discrete depths during the January 6–12, 1978 cruise. The zoeae were more abundant at the surface by night and at 15- and 25-m depths by day (Table 8); using the multi-way contingency table method, day versus night densities at these levels were significantly different ($P = 0.01$).

Horizontal dispersal was evident during the early zoeal stages. On the Farallon Islands transect on January 14, 1976, all stage I zoeae were found between 13 and 26 km from shore. Two weeks later they occurred from 1 to 42 km from shore, although densities within 13 km were low.

Our March 1978 cruise was conducted after a large plume of estuarine water had entered the Gulf (Figure 22). At this time, we found only stage I and II zoeae in Gulf samples, all at low densities. All stage II zoeae were associated with water in which surface salinity was greater than 32 ppt, even though approximately 50% of the Gulf surface water ranged in salinity from 23.2 to 31.7 ppt. In laboratory studies, salinities within this range did not adversely affect larval survival (Reed 1969). Thus, low salinity probably did not cause mortality in the

Gulf, but advancement of estuarine water apparently aided offshore movement of zoeae.

TABLE 8. Densities (No./100m³) of Dungeness Crab Stage I Zoeae in the Gulf of the Farallones, January 6-12, 1978.

Station no. (Figure 14)	Day samples				
	Surface tow	5-m tow	15-m tow	25-m tow	Oblique tow
917	1	—	2	0	2
1007	0	1	22	24	30
1116	0	3	95	—	89
1165	10	14	544	486	160
1216	3	3	22	8	18
1241	0	0	0	0	0
1414	4	17	225	16	171
1639	0	0	0	0	0
1709	128	92	189	70	74
1757	3	32	52	16	2
1804	0	0	0	0	0
1851	0	0	0	0	0
Night samples					
784	26	1	3	7	7
824	3	4	3	6	21
864	12	2	3	4	15
874	22	5	0	—	4
906	0	0	0	0	0
961	169	28	2	24	87
1053	0	1	0	0	1
1068	30	2	0	—	20
1100	0	0	0	0	0
1299	0	2	0	—	0
1332	0	1	0	5	8
1357	217	15	18	26	—
1390	0	0	0	0	0
1472	31	13	16	1	18
1529	0	0	0	0	0
1552	0	0	0	—	0
1584	0	0	0	0	0
1607	5	11	1	—	20
1660	9	9	9	56	43
1819	1	0	0	7	0
1865	6	0	1	—	0
1274	1	0	0	0	3

We observed similar results during December 1979 and January 1980 when substantial rainfall and Delta outflow caused an extensive plume of estuarine water in the Gulf (Reilly, Chapter 5). On the December 27, 1979 transect to the Farallon Islands, no stage I zoeae were found within 20 km seaward of the Golden Gate Bridge but maximum densities occurred 25 to 35 km seaward. The plume extended into the Gulf approximately 15 to 20 km. On January 21, 1980, the plume had advanced to 40 km seaward. Stage I densities had decreased from 32 to 56/100 m³ to 3 to 8/100 m³; most of the zoeae probably had molted to stage II by then. We only collected stage II zoeae seaward of the plume at our most distant station.

Continued movement of zoeae out of the Gulf was evident as the stages progressed (Figure 30). During the entire study, we collected only 65 stage III, 26 stage IV, and 10 stage V zoeae inshore of the 500-fm (915-m) depth contour which lies approximately 10 km seaward of the Farallon Islands. No stage V zoeae were found within 36 km of shore. On March 3, 1979, at a station 4 km seaward of the Islands, densities of stage I, II, III, and IV zoeae were 4, 13, 15, and 5/100 m³, respectively.

To determine whether scarcity of late-stage zoeae in our Gulf samples could be due to zoeae descending to the ocean floor, which previous plankton tows probably had not sampled adequately, we conducted 27 bottom tows with the plankton sled during March and April 1978 cruises and one additional tow in April 1980. Although *Cancer* larvae occurred in these tows at densities as high as 2,090/100 m³, no Dungeness crab larvae were found. No late-stage Dungeness crab zoeae were collected in any plankton tows in the Gulf in 1978 and 1980. Thus, we could not compare bottom and oblique tows. In fact, late-stage zoeae were absent from Gulf waters during most of our sampling.

Megalopae

Although late stage zoeae were most abundant offshore, we frequently collected megalopae at routinely sampled Gulf stations from April to June (Figure 30). In 1976, 14 megalopae were captured in the Gulf, all in the northern section. In April 1977, we captured 366 megalopae. The highest densities occurred in the Gulf within 15 km of Pt. Reyes. Surface isotherms during the same period showed colder water entering the Gulf from the north (Figure 21). It is possible that megalopae were transported into the Gulf with it. In May 1977, and April and May 1978, our total catch of 20 megalopae again came from the northern Gulf. In June 1977, we dipnetted more than 500 *V. veleva* from Gulf surface waters. Although these coelenterates occurred throughout the Gulf, those carrying megalopae were only found north of the entrance to San Francisco Bay and within 20 km of shore. During the April–May 1979 cruise, which extended to the Bodega Bay area in the northern Gulf, relatively high densities of megalopae again occurred within 15 km of Pt. Reyes. Megalopae also occurred at relatively high densities north of Pt. Reyes within 10 km of shore. One station yielded 306 megalopae in a 10-min surface tow (139/100 m³). Few or no megalopae were found at stations farther seaward. During the April 1980 cruise, we sampled stations to 50-km seaward of Bodega Bay and megalopae occurred only within 31 km of shore.

In April 1979, we conducted a series of night-light stations from our research vessel. In Drakes Bay (Figure 17) the light attracted an estimated 100,000 megalopae within an hour's time on each of two successive nights. Smaller numbers were attracted in Bodega Bay and central San Francisco Bay and a few were observed near Southeast Farallon Island.

In the southern Gulf, station 961 (Figure 14), 24 km from shore, yielded good catches of megalopae on three occasions. Surface tow densities during the April 1977 and April–May 1979 cruises were 14 and 21/100 m³, respectively. We also dipnetted 100 *V. veleva* at this station on April 30, 1979 and found 50 megalopae, the highest ratio of megalopae to *V. veleva* we observed during the study. However, most southern Gulf stations generally yielded few or no megalopae



FIGURE 30. Distribution of Dungeness crab stage III, IV, and V zoeae and megalopae in the Gulf of the Farallones, 1975–1980.

Day vs. Night Distributions. Thirty-four Gulf stations were occupied during the April 1977 cruise when 366 megalopae were collected. We sampled 12 stations, once by day and once by night, to determine vertical distribution of megalopae. We statistically compared megalopal densities for day versus night surface and oblique tows (Table 9) using Student's t-test. Day and night surface tow densities were not significantly different, nor were day and night oblique tow densities. However, day surface tow densities were significantly greater than day oblique tow densities ($P=0.05$) and night surface tow densities were significantly greater than night oblique tow densities ($P=0.01$). In April 1980, at a night station 4 km west of Bodega Bay, a series of discrete-depth tows at the surface, 5 m, 15 m, 25 m, and an oblique tow yielded megalopal densities (no./100 m³) of 3.7, 15.8, 5.6, 0.0, and 2.5, respectively. These data show that megalopae occur more frequently in the upper 15 m of the water column. Their vertical distribution differs from that of stage I zoeae in that relatively high densities of megalopae occur in the upper 15 m during both day and night.

TABLE 9. Densities (No./100 m³) of Dungeness Crab Megalopae in the Gulf of the Farallones, April 6-11, 1977.

Station	Day		Night	
	Surface	Oblique	Surface	Oblique
784	0	0	0	0
864	0	0	1	1
961	14	4	0	0
1053	0	0	1	1
1165	9	0	1	5
1274	1	1	0	1
1390	1	1	0	0
1529	22	0	33	6
1639	1	1	2	0
1660	43	3	13	1
1757	0	1	26	4
1851	0	0	0	0

As megalopae approach the molt to the juvenile stage, they settle to the bottom. Although megalopae were found throughout the Gulf, they were found at the bottom primarily in the nearshore zone and occasionally in the Bay. Although their presence in stomachs of demersal fishes indicates that settling occurred to a maximum bottom depth of 60 m (Figure 31), of 995 megalopae taken from demersal fish stomachs outside the Bay, 965 occurred at stations with depths less than 25 m, including samples from the Pt. Reyes-Bodega Bay area.

We collected 97 megalopae in plankton tows in central San Francisco Bay between the Golden Gate Bridge and the Richmond-San Rafael Bridge. One megalopa in the stomach of a Pacific staghorn sculpin, *Leptocottus armatus*, collected near Pinole Point in San Pablo Bay represents the maximum penetration into the Bay in our samples. We did not have sufficient data to determine the statistical significance of megalopal densities in surface and oblique tows in the Bay. However, on May 6, 1979, at a station near the Golden Gate Bridge, an oblique tow yielded 44 megalopae compared to only four megalopae in a surface tow of similar duration. This suggests that megalopae may be carried into

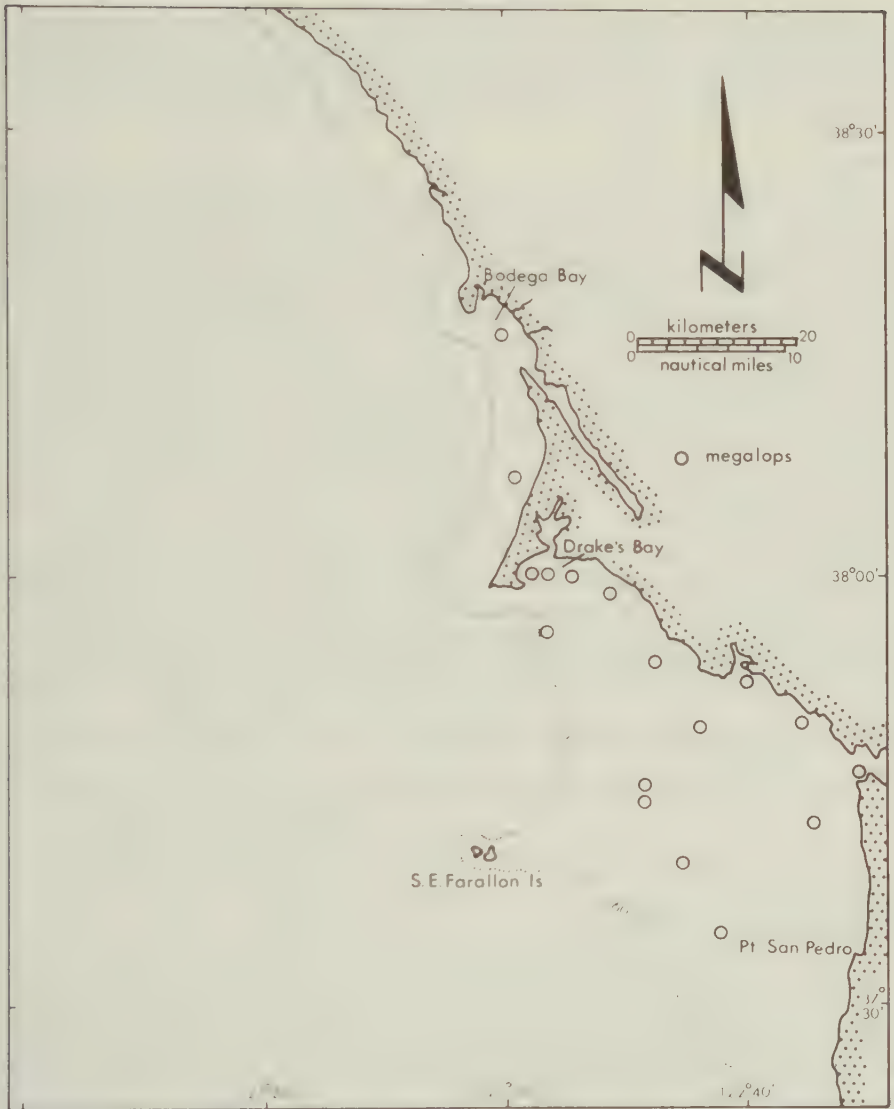


FIGURE 31. Distribution of newly settled Dungeness crab megalopae from Bodega Bay to Pt. San Pedro, based on fish stomach analysis, 1975-1979.

the Bay by bottom currents after settling in the Gulf or that they descend from surface waters as they enter the Bay.

Distribution of Larvae From the Gulf to Northern California

One cruise conducted in March 1979 (Figure 17) provided much of the data from which distributions of various stages in northern and central California were determined. This cruise, conducted from the Gulf to Cape Mendocino and to 100 nautical miles (185 km) seaward, collected all Dungeness crab larval stages

including 11 stage I, 19 stage II, 129 stage III, 103 stage IV, and 681 stage V zoeae, and 18 megalopae. Before 1979, we did not encounter any stage V zoeae in the Gulf study area. The March 1979 cruise extended farther offshore and apparently coincided with a peak occurrence of stage V zoeae in California.

Zoeae

Offshore Dispersal. The pattern of larval distribution demonstrated substantial offshore dispersal as zoeal stages progressed (Figures 32 and 33). All stage I and II zoeae were found within 50 km of shore while stages III–V extended to 185 km from shore. Maximum offshore dispersal was apparent during stage III. We collected stage II and III zoeae at relatively high densities off Cape Mendocino at one station over the continental shelf where we observed a well-defined color change in the surface water. The salinity inshore of the boundary was 0.5 ppt less than that immediately seaward. This may have been the boundary of coastal water diluted by winter rain and runoff; early-stage zoeae occurred seaward of it. Stage V zoeae were collected at stations 24 to 186 km from the coast but were most abundant from 40 to 150 km. They occurred farther from shore off Cape Mendocino and Pt. Arena than in the vicinity of the Gulf.

Relative age of stage V zoeae on this March 1979 cruise, as determined by readiness to molt also suggests continual offshore dispersal of zoeae. Readiness to molt was determined by examination for withdrawal of tissue from the exoskeleton, particularly in dorsal and rostral spines and the telson. Larger percentages of stage V zoeae close to molting were found farthest from shore (Table 10).

TABLE 10. Percentages of Dungeness Crab Stage V Zoeae Close to Molting, March 20–29, 1979.

	<i>Distance from shore (km)</i>			
	<i>0–50</i>	<i>51–100</i>	<i>101–150</i>	<i>> 151</i>
Number collected	40	550	74	17
Percentage (%) close to molting	17.5	18.7	40.5	35.3

Of 168 stage V zoeae collected in oblique tows during this cruise, 98.8% occurred at stations with depths in excess of 500 fm (915 m), while 72% of the stations sampled had depths greater than this. A step-wise multiple regression analysis was performed with stage V zoeal density as the dependent variable and station depth, latitude, distance from shore, time of day, surface temperature, surface salinity, 25-m temperature, and 25-m salinity as independent variables. A coefficient of multiple determination (r^2) of 0.18 was obtained with all independent variables included in the regression. Among the independent variables, depth contributed most to the overall r^2 ($\Delta^2=0.11$), followed by latitude ($\Delta^2=0.04$). However, the overall low r^2 indicates that very little (18%) of the variation in offshore dispersal is explained by these variables.

Limited data from stations sampled off Eureka (Figure 15) from 1977 to 1980 also indicate offshore dispersal of larvae. In March 1978, for example, all stage V zoeae occurred seaward of the continental shelf, over the continental slope (depth 200 to 1,000 m). However, the Eureka transects extended only 53 km seaward, and it is likely that we sampled only part of the offshore range of the

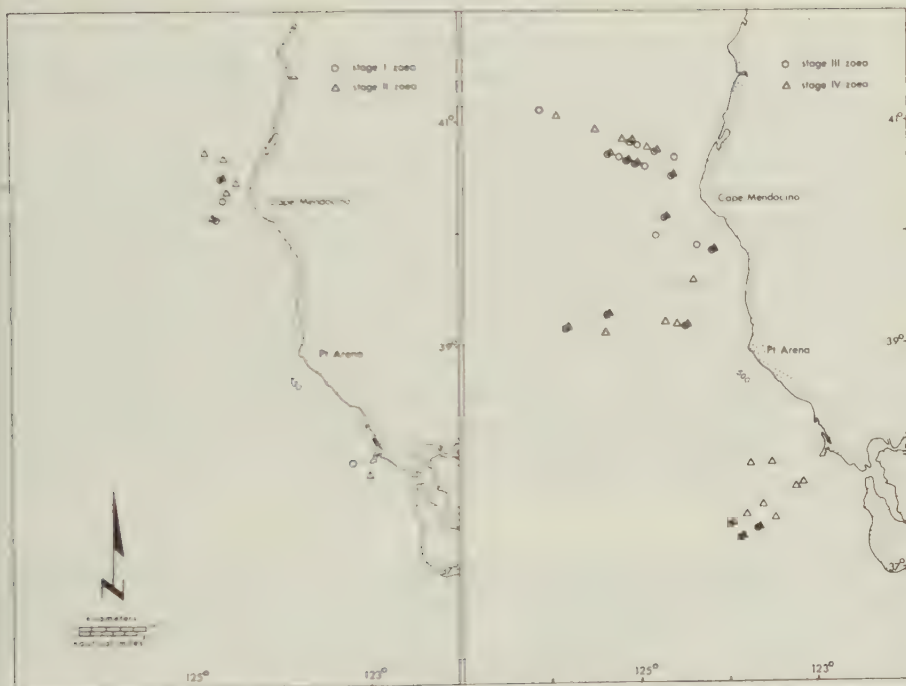


FIGURE 32. Distribution of Dungeness crab stage I, II, III, and IV zoeae in central and northern California, March 20-29, 1979.



FIGURE 33. Distribution of Dungeness crab stage V zoeae and megalopae in central and northern California, March 20-29, 1979.

late-stage zoeal population in that area.

The fact that nearly all stage V zoeae were collected seaward of the continental shelf does not imply a causal relationship with water depth, but is most likely a result of dispersal by ocean currents.

Diel migration. Night surface tows were conducted at 25 stations during the late March 1979 cruise. Densities of stage V zoeae at two of these stations, one 75 km seaward of Pt. Arena and the other 74 km seaward of Cape Mendocino, were 374 and 154/100 m³, respectively. Only four daytime surface tows were conducted at stations within the range of occurrence of stage V zoeae and no larvae were found. At one night station in which stage V zoeae were collected at the surface (9/100 m³), none were found in tows at 5, 15, and 25 m. The highest densities of stage III (45/100 m³) and IV (34/100 m³) zoeae observed during the study also occurred in night surface tows. Although we did not have sufficient data to test statistically for vertical migration, it appears that late-stage zoeae exhibit similar diel behavior as stage I zoeae in that they occur more frequently in surface waters by night than by day.

Megalopae

All 18 megalopae collected during the March 1979 cruise had molted recently, as evidenced by soft exoskeletons. Megalopae were more abundant in surface than in oblique tows and occurred from 34 to 148 km from the coast. By contrast, 1 month later we found megalopae aggregated nearshore.

CalCOFI Samples

Results from the CalCOFI collections must be considered in the context of their sampling plan, which was designed as a fish egg and larval survey that extended more than 1,000 km from the coast, and in which collection efforts were less intense in the nearshore zone than in our study. Nevertheless, CalCOFI results support our observations. Most Dungeness crab larvae (>98%) occurred within 200 km of shore and distribution of the larvae provides further evidence of offshore drift during zoeal development with subsequent inshore movement of the megalopae (Figures 34, 35, and 36). Only 10 of 733 stage I zoeae were collected seaward of the 500-fm (915-m) depth contour, while 109 of 110 stage V zoeae were found in this range. Substantial drift offshore, to 143 km, was observed for zoeal stage II. The occurrences of one stage III zoea 235 km seaward and one megalopa 296 km from shore exemplify the potential offshore drift that may occur during larval development. By contrast, only one of 57 megalopae collected in March was found within 90 km of shore, while 77 of 82 megalopae occurred there in April.

Relative Abundance of Larvae

Maximum Densities by Stage

The terms "low" and "high" have been used frequently in this chapter to describe larval densities. A summary of maximum densities from oblique tows for each larval stage (Table 11) may serve to define the above terms and allow comparisons between years and with other studies. The maximum oblique tow density (896/100 m³) of stage I zoeae in 1976 (Table 11) was the highest density



FIGURE 34. Distribution of Dungeness crab stage I and II zoeae in central and northern California from CalCOFI samples, 1949-1975.

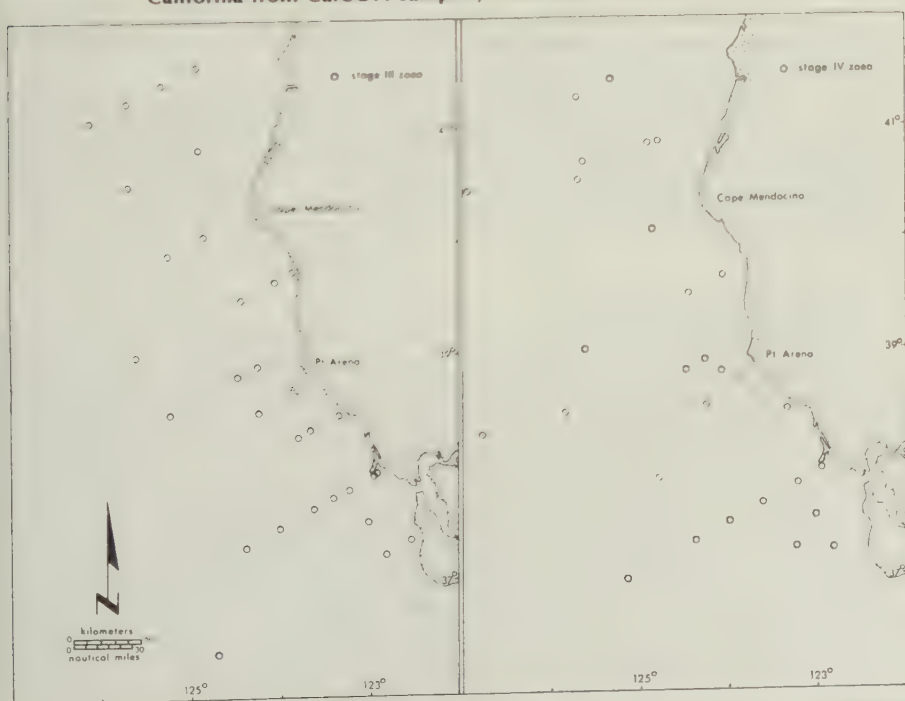


FIGURE 35. Distribution of Dungeness crab stage III and IV zoeae in central and northern California from CalCOFI samples, 1949-1975.

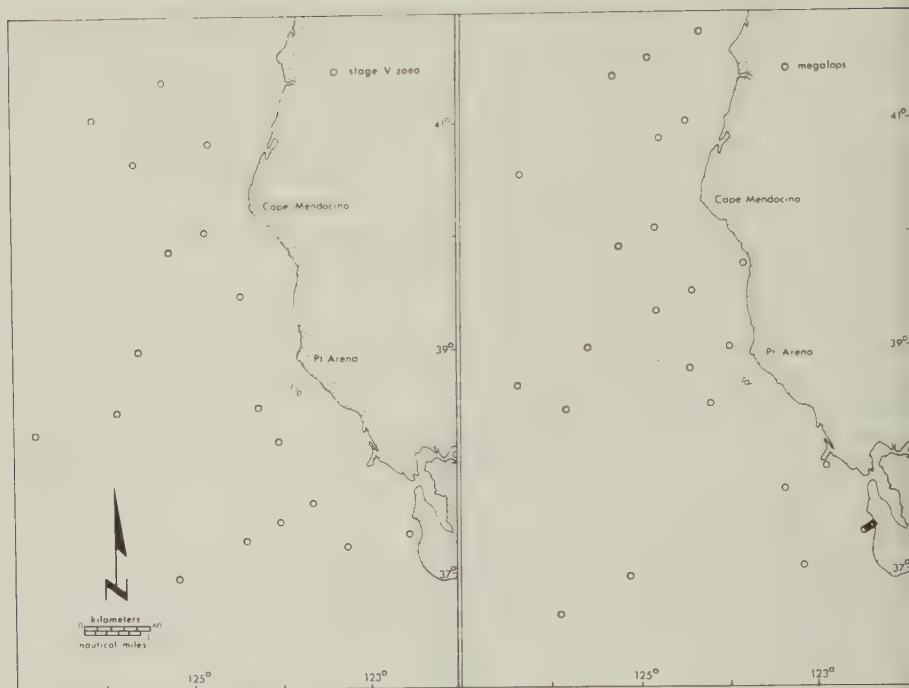


FIGURE 36. Distribution of Dungeness crab stage V zoeae and megalopae in central and northern California from CalCOFI samples, 1949–1975.

of Dungeness crab larvae we collected. However, a 15-m tow in January 1978 yielded stage I zoeae at a density of 544/100 m³.

Discrete depth tows at times resulted in considerably higher densities than oblique tows, reflecting vertical distribution of larvae. For example, maximum densities of stage V zoeae and megalopae, observed in surface tows in 1979 were 374 and 139/100 m³, respectively, compared to 14 and 16/100 m³ in oblique tows in 1978 and 1979, respectively (Table 11).

Sampling Variability

The distribution of planktonic organisms is non-random and usually patchy (Cushing 1962; Barnes and Marshall 1951) and considerable variability often occurs in plankton samples. To analyze for variability in our samples, five replicate oblique tows were taken at each of three stations during the night of January 12, 1978. The tows were conducted sequentially at 10-min intervals while the ship circled. A normalizing logarithmic transformation was performed on the data and 95% confidence limits were determined for mean densities of stage zoeae in the tows (Table 12). The unusually high standard deviation in our data from station 1165 resulted from the absence of stage I zoeae in one of the tows. Subsequent analysis indicated that zoeae occur more abundantly in surface waters at night and, thus, oblique tows would have a greater probability of missing surface "patches" of zoeae than surface tows. However, results from

TABLE 11. Maximum Densities (No./100m³) of Dungeness Crab Larval Stages Collected by Oblique Plankton Tows (GF = Gulf of Farallones; EK = Eureka Area; SF = San Francisco Bay Complex; PA = Pt. Arena; BB = Bodega Bay Area).

	Zoeal stage I		Zoeal stage II		Zoeal stage III		Zoeal stage IV		Zoeal stage V		Megalopa	
	Density	Area	Density	Area	Density	Area	Density	Area	Density	Area	Density	Area
1975	NS*		NS		NS		NS		NC†		1	GF
1976	897	GF	44	GF	1	GF	1	GF	NC		4	GF
1977	NS		NS		11	EK	5	EK	NC		10	GF
1978	171	GF	6	GF	4	GF	2	EK	14	EK	2	GF, EK
1979	447	GF	51	EK	30	EK	5	GF	5	EK	16	SF
1980	290	EK	NS		NS		NS		NS		3	BB
CalCOFI	78	GF	165	GF	18	GF	3	GF	3	PA	5	GF

* NS = Primary larval period not sampled.

† NC = None collected.

stations 1068 and 1116 are within the range of variability for individual crustacean species reported by other workers, as summarized by Wiebe and Holland (1968). Our sampling effort proved adequate to show differences of at least one order of magnitude.

TABLE 12. Sampling Variability of Stage I Zoeae from Replicate Oblique Plankton Tows in the Gulf of the Farallones, January 12, 1978 ($x = \text{No.}/100 \text{ m}^3$; $y = \log_{10} x$).

Tow number	Station 1068		Station 1116		Station 1165	
	x	y	x	y	x	y
1	32.7	1.515	5.9	0.771	1.0 *	0.000
2	17.1	1.233	8.7	0.940	29.1	1.464
3	16.5	1.217	9.0	0.954	22.8	1.358
4	17.6	1.246	8.9	0.949	28.6	1.456
5	14.7	1.167	5.6	0.748	22.3	1.348
Sum.....	98.6	6.378	38.1	4.362	103.8	5.626
Mean	19.72	1.276	7.62	0.872	20.76	1.125
SD		0.137		0.103		0.665
95% CL.....		41.6-240%		51.8-193%		1.43-6.998%

* Due to zero density in this tow, the transformation of $\log (x + 1)$ was used for all tows at station 1165.

Relationship to Water Temperature

An inverse relationship was observed between relative abundance of stage I zoeae in the Gulf and water temperature. The highest density of stage I zoeae we collected occurred in January 1976 when Gulf temperatures during December 1975-January 1976 (Table 7) were colder than any other December-January period during the study. Gulf temperatures during December 1976-January 1977 were warm and, although we began sampling in January, we missed the peak stage I zoeal period which was early that year. The 1979 larval year class, the strongest during our studies, also hatched in relatively cold water, while the 1978 and 1980 year-class hatches occurred during warmer conditions and resulted in lower larval production. Student's *t*-test was used to compare mean densities of stage I zoeae from oblique tows taken on Golden Gate-Farallon Islands transects from 1976 to 1980 using the transect that produced the best catch each year. There was considerable variability in individual samples and the only statistically significant difference was that mean density for 1976 was greater than that for 1980 ($P=0.05$, $t=2.35$, $d.f.=10$).

Central California vs. Northern California

On January 22, 1980, stage I zoeae occurred at a maximum density of 290/100 m^3 off Eureka, while the highest density in the Gulf for the 1980 larval year class was 56/100 m^3 on December 27, 1979. In March 1979, transects (20 to 30 stations each) to 185 km seaward off Cape Mendocino, Pt. Arena, and the Gulf yielded average densities of stage V zoeae in oblique tows of 1.3, 0.7 and 0.4/100 m^3 , respectively. These data suggest that zoeal abundance may be directly related to the magnitude of the spawning stock which presumably is larger in northern California.

Stage I Zoeae vs. Megalopae in the Gulf

The relative abundance of stage I zoeae and megalopae in the same year class in the Gulf were not consistently related. We sampled too late in 1975 and 1977 larval seasons to estimate adequately stage I zoeal densities. In 1976, stage I zoeal densities were high, but the catch of megalopae was poor. In 1979, stage I zoeae and megalopae were relatively abundant, while in 1978 and 1980 densities of both were low.

Megalopae vs. Juveniles

The relative abundance of megalopae was consistently related to strength of the new year class of post-larval crabs in the Gulf and the Bay (Tasto, Chapter 9; Reilly, Chapter 10). Juvenile year classes in 1976 and 1978 were relatively weak and catches of megalopae also were poor in both years. Stronger juvenile year classes occurred in 1977 and 1979 when megalopal abundance also was high. During the peak megalopal period (estimated from highest catches), the average density for surface tows in the Gulf was 4.1 and 0.1/100 m³ in 1977 and 1978, respectively. In the Pt. Reyes-Bodega Bay area the average density for surface tows during April–May 1979 was 18.6/100 m³. Limited data suggest that the 1980 year class of megalopae was weak; average surface tow densities during our April 1980 cruises in the Fort Bragg and Bodega Bay-Pt. Reyes areas were 0.3/100 m³ and 0.5/100 m³, respectively.

CalCOFI Samples

Data from CalCOFI samples (Table 5) were sparse when considered in the context of time and geographical area. Thus, no definite conclusions could be reached concerning pre- and post-decline years or geographical variations in abundance.

DISCUSSION

Timing of Larval Occurrences

We observed the peak hatching period of Dungeness crab larvae in the Gulf of the Farallones to vary from late December to early January. Hatching was early when temperatures during the December–January period were warm and later when they were cool. Laboratory studies with ovigerous Dungeness crabs verify this inverse relationship between water temperature and both egg development and hatching times (Wild, Chapter 16).

Larval development time also has been shown to be inversely related to water temperature (Poole 1966; Reed 1969). Reed (1969) reported a development time of approximately 90 days to the megalopal stage at 10 C and 25 to 30 ppt salinity. Complete larval development time in Poole's laboratory studies with water temperature constant at 10.6 C was 111 days. However, only one of his larvae reached the first post-larval instar. Gaumer (1969) found that 109 days were needed at 11 C to complete larval development. Lough (1974) observed the peak appearance of stage I zoeae in mid- to late January in Oregon waters. He estimated length of the larval period to average approximately 130 days. Because winter temperatures in central California generally are 2 to 3 C warmer

than in Oregon waters, my estimate of the length of the larval period (105 to 125 days) appears to be reasonable.

Distribution

Horizontal Dispersal

Most Dungeness crab larvae in central California hatch and complete their early zoeal development during the Davidson Current period when the general pattern of circulation along the coast has a net northward movement (Reid and Schwartzlose 1962; Pirie and Steller 1977). We were not able to discern northward or southward (alongshore) drift of larvae in our samples; however, Lough (1976) concluded that northward larval transport, based on the average speed of the Davidson Current in Oregon waters, could be up to 150 miles (280 km) per month.

We found that considerable offshore movement of larvae occurs during zoeal stages II-V. The larvae appear to be transported seaward from the onset of hatching, but most molt to the second zoeal stage before reaching the continental slope. Offshore movement of zoeae appears to be aided by estuarine runoff and possibly also by upwelling, especially for late stages in the Pt. Arena and Cape Mendocino areas. Geostrophic flow offshore may occur throughout the year in central California north to Cape Mendocino (Richard Parrish, NMFS, pers. commun.).

The factors influencing larval distribution north of Cape Mendocino are less clear. We found zoeae to be farther from shore in northern than in central California, yet onshore flow occurs during January and February north of Cape Mendocino (Richard Parrish, NMFS, pers. commun.). It seems possible that some larvae occurring in northern California waters in March could have hatched in central California and were transported offshore by estuarine runoff and carried northward by the Davidson Current. Gaumer (1971) theorized that larvae hatching in northern California in December could be carried northward to British Columbia by the time they settled out.

Studies of larval distribution in Oregon contrast in part with results of our study. Peterson et al. (1979) concluded that surface waters are transported northward and onshore from October to March in Oregon. Lough (1976) found the majority of early stage Dungeness crab larvae within 10 miles (16 km) of shore and attributed this to retention by an onshore component of the Davidson Current. However, Lough (1974) found stage III-V zoeae and megalopae at stations 45 to 60 miles (72 to 96 km) from shore which also suggests offshore drift similar to results from our study. Lough did not capture any Dungeness crab stage V zoeae within 16 km of shore. He reasoned that the volume of water filtered at inshore stations was inadequate and that late-stage zoeae may be associated with the ocean bottom. We did not collect any Dungeness crab larvae in bottom tows with the plankton sled in the Gulf in March and April 1978 or April 1980.

Our results demonstrate the recruitment of megalopae to nearshore ocean waters of central California following a period in which stage V zoeae were generally absent within 40 km of shore. Lough (1974) observed large numbers of megalopae within 10 miles (16 km) of the Oregon coast during April and May

in 1970 and 1971. In 1975, Wickham (1979b) dipnetted *V. veleva* seaward of Bodega Bay to 24 km and found megalopae only on those within 10 km of shore. In May 1976, Wickham (1979b) observed two distinct bands of megalopae in surface waters 1 and 8 km offshore of Bodega Bay with an estimated average density of $1/\text{m}^2$. More recently, aging of megalopae by intermolt staging (Hatfield, Chapter 7) has provided further evidence of inshore transport. Megalopae that were more advanced in their development occurred closer to shore and in San Francisco Bay in central California.

We were unable to determine the mechanism for inshore transport of megalopae which occurs at a time when offshore Ekman transport of surface waters induced by northwesterly winds is common. Studies by Bourke et al. (1971) off Oregon, indicate that wind-driven water motion may extend to a depth of 10 m and that flow in the Eckman surface layer is offshore. Hachey and Fothergill (1953) found that winds greater than 10 mph will influence the magnitude and direction of surface currents, but that a given surface current is a complex mixture of wind current, tidal current, and semi-permanent current. In central California, the arrival of megalopae in nearshore waters generally occurs in April after the onset of predominantly northwest winds in March (Figure 24). From April to June, winds blow predominantly from the northwest with Ekman transport directed offshore which makes it difficult to understand how megalopae become aggregated nearshore. The formation of counter-clockwise eddies in the vicinity of headlands during the upwelling period is a possible explanation.

Northwesterly winds blowing toward the coast in the spring cause rafts of *V. veleva* to wash ashore in central California (Wickham 1979b); megalopae are often found attached to them. We have found the occurrence of these hydroids in central California to be sporadic. Therefore, although they occasionally may be of importance as inshore transporters, they could not account for the annual recruitment of megalopae. Recruitment from the north could explain the presence of megalopae in the Gulf in June 1977 after a major period of settling and molting to the juvenile stage had occurred in early April. Dipnetting of *V. veleva* in June yielded an average of 1 megalopa/10 *V. veleva* in the northeastern section of the Gulf, an area of approximately $1 \times 10^9 \text{ m}^2$. Although we did not estimate the average density of *V. veleva*, a conservative value of $1/100 \text{ m}^2$ would indicate that almost 1 million megalopae were present on *V. veleva*. At a maximum speed of 20 km/day (Schwartzlose and Reid 1972), the California Current could transport megalopae from the Oregon border to Pt. Reyes during an average 25-day megalopal period. Temperatures south of Cape Mendocino during the spring of 1977 were colder than in any other year of the study; this would prolong development and extend southerly transport.

Larvae of the anomuran sand crab, *Emerita analoga*, frequently co-occurred with Dungeness crab larvae in offshore samples from the CalCOFI collection and our study (Hatfield, Chapter 8). Efford (1970) discussed several aspects of the planktonic life history of *E. analoga* which closely parallel those of the Dungeness crab. Development time from hatching to settling is approximately 4 months and megalopae begin to arrive on California beaches in large numbers by April. He proposes a hypothesis in which larvae drift from one current to another and back again via interconnecting eddies. In this manner many would be retained nearshore. No evidence, however, is presented from plankton samples to support this concept.

Mayer (1973) related the recruitment of megalopae into Similk Bay, Washington to tidal and density currents. The megalopae that occasionally enter central San Francisco and San Pablo Bays most likely are transported by density currents of high-salinity bottom water. The vertical extent of these currents is not known, but we observed a halocline at approximately 5 m in the Gulf near the Golden Gate during periods of high Delta outflow. Conomos et al. (1970) found that seabed drifters released within 25 km of the Bay entrance moved into the Bay.

Sandifer (1973 and 1975) noted that many species of decapod larvae in Chesapeake Bay were more abundant in the lower layer of the water column where net transport is upstream. This distributional adaptation would retain them in the estuary. *C. irroratus* larvae were occasionally found in low concentrations in the Bay. However, he found no tendency for *C. irroratus* larvae to concentrate near the bottom; surface and bottom concentrations were 44.3% and 55.7%, respectively. No megalopae or stage V zoeae were collected. Apparently most *C. irroratus* larvae hatch offshore and some are retained within the Bay by chance only. Sandifer concluded that the Chesapeake Bay population is apparently restocked by migration of animals from the inner-shelf area. Bigford (1979) speculated that passive migration of *C. irroratus* stage V zoeae, megalopae, and juveniles, aided by bottom currents, is a major factor in recruitment to Chesapeake Bay. We found high densities of Dungeness crab stage V zoeae in night surface tows offshore and aggregations of megalopae in the upper layer of the water column nearshore and occasionally in San Francisco Bay.

Vertical Migration

Analysis of our field data shows that stage I Dungeness crab zoeae undergo diel vertical migration; they were captured more frequently near the surface by night and at 15- and 25-m towing levels during the day. The data also suggest that later zoeal stages have a similar diurnal distribution. These behavioral adaptations may be related to observed patterns of dispersal and aggregation. During early zoeal development in winter, nights are longer than days and larvae would thus spend more time in surface waters. They would then be influenced more by estuarine runoff and would be transported offshore. In contrast, we observed the highest densities of megalopae in the upper 15 m both day and night in the nearshore area. It is unclear how this change in vertical orientation affects their horizontal distribution.

In laboratory studies, Gaumer (1971) reported that Dungeness crab zoeae and megalopae displayed positive phototaxis to light intensities of 25 and 240 ftc and a negative response to 990 ftc. Megalopae exhibited the strongest negative response to the water surface or light. He predicted that larvae in the ocean would approach the water surface at night and the opposite response should be expected during daylight hours. However, he implied that the megalopal response may be a trait of cultured megalopae and reported field observations of megalopae actively swimming on the surface in Yaquina Bay, Oregon during the day.

Jacoby (1980) tested responses of Dungeness crab larvae to light intensities of 4, 20, 90 and 4500 ftc. The latter corresponds to full sunlight at the ocean surface in central California. Stage III, IV, and V zoeae moved toward brighter light than stages I and II, but megalopae moved only toward the dimmest light.

unless pressure was increased. However, megalopae never moved toward the brightest light.

Jacoby found that all Dungeness crab larval stages could detect gravity and pressure changes but that their responses were too inconsistent to predict field behavior. Bigford (1977 and 1979) reported that stage I and III *C. irroratus* were geonegative and stages II, IV and V were geopositive without directional light or increased pressure. Megalopae remained on the bottom of the experimental chamber. He observed a "pre-megalopal" behavior pattern as the fifth stage progressed in which depth maintenance by swimming was reduced gradually.

Larval Abundance and Sampling Variability

I did not find a consistent relationship between larval abundance and subsequent recruitment to the commercial fishery for a given year class. We began sampling stage I zoeae in January 1976. This relatively strong zoeal year class, which was followed by weak megalopal abundance, contributed to the fishery during the 1978–79 and 1979–80 seasons; the 1977 larval year class with highest megalopal abundance contributed to the fishery in 1979–80 and 1980–81, assuming 3 and 4-year lag times. Landings were above average for northern California and remained low in central California (Figure 10). Gregory Lough (Oregon State University, unpublished manuscript) could not relate Dungeness crab larval abundance in 1970 and 1971 to commercial landings in Oregon. Mean abundance of early-stage zoeae at four inshore stations in Lough's study was 680 and 190/100 m³ in 1970 and 1971, respectively. These are in the same order of magnitude as maximum stage I zoeal densities in 1976 and 1979 in the Gulf. Lough found that Oregon crab landings in 1974 and 1975 were extremely low and similar for these 2 years. Compounding our problem is lack of knowledge of the ultimate destination of larvae produced in the Gulf. If larvae return to the area of hatching, then comparisons of stage I zoeal densities between areas may be valid. On the other hand, larval production in the Gulf may contribute to recruitment in northern California and (or) some may be lost by offshore drift.

We attempted to minimize sampling variability by using larger mesh for collecting late-stage zoeae and megalopae, thereby reducing avoidance, using flowmeters to determine the amount of water filtered, and sampling frequently to minimize effects of non-random spatial distribution of larvae. Variability in our sampling results was small enough to enable us to discern differences in average larval densities of at least one order of magnitude. Lough (1974) conducted six replicate tows at one station in Oregon waters and reported 95% confidence limits of 4 to 2484% for seven species of brachyurans. He attributed this wide range to the low number of larvae collected. No Dungeness crab larvae were found in these tows. Series of duplicate tows the same year yielded more narrow limits (e.g. 44 to 230% for *C. oregonensis* stage II zoeae), although the range for Dungeness crab megalopae, 3 to 3227%, was high. Confidence limits for single observations for individual crustacean species, summarized by Wiebe and Holland (1968), ranged from 14.3–698% to 59–169%. Confidence limits for two of our three sets of replicate tows for stage I Dungeness crab zoeae (Table 12) were within this range.

We found a direct relationship between stage I zoeal production, relative abundance of megalopae, and resultant strength of year classes of juvenile crabs

in 1978 and 1979, but in 1976, zoeal production was high and recruitment of megalopae and juveniles to the Gulf and Bay was low. However, Wickham (1979b) found megalopae to be abundant in waters off Bodega Bay in 1976. It is possible that large numbers of megalopae were transported from the north to the Bodega Bay area but did not penetrate farther south into the Gulf, or that our sampling missed the major period of recruitment of megalopae in the Gulf that year. However, results of stomach content analysis of demersal fishes (Reilly, Chapter 10) indicate that our sampling effort did not miss the major period of recruitment into the Gulf; very few young-of-the-year juvenile crabs were found in the stomachs of fishes collected in the Gulf and Bay that year.

Several other studies have investigated relationships between larval production of commercially important Crustacea and spawning stocks. For example, Scaratt (1964) sampled American lobster, *Homarus americanus*, larvae in coastal Canadian waters from 1949 to 1961 and could find no conclusive relationship between larval and subsequent stock abundance, although he concluded that there was a possible direct relationship between abundance of stage I larvae and parent stock density. An estimate of total abundance of stage I larvae of the lobster *H. gammarus* was calculated by Nichols and Lawton (1978) for a portion of coastal England. Their estimate was extremely low when compared with the potential from the available breeding stock (ovigerous females) for that year.

CONCLUSIONS

Our primary goal was to identify life history stages of the Dungeness crab that are critical to high recruitment and survival in the Gulf of the Farallones and San Francisco Bay. These areas provide habitat for crabs which are recruited into the San Francisco area commercial fishery. We consider a "critical" stage to be one during which a year class of crabs suffers sufficient mortality or displacement so that relative abundance of subsequent stages results in a small population and low fishery landings.

The most consistent relationship we observed during the study was that the relative abundance of megalopae was directly related to the subsequent year class of juvenile crabs. Most of the megalopae we collected nearshore were in advanced stages of development (Hatfield, Chapter 7). Thus, if a relatively large number of larvae reach the late megalopal stages, a good year class of juvenile crabs should result. Therefore, the late megalopal to early juvenile instar period does not appear to be a "critical stage". One indication of the potential recruitment of megalopae to nearshore areas was an observation by Lough (1974) of an oblique plankton tow density of 800/100 m³ in Oregon waters. This is 50 times greater than the maximum density we found in any oblique tow in our study area. It is possible that present recruitment levels of megalopae, although varying substantially during the study, are still one or more orders of magnitude below that necessary to sustain the commercial fishery at historic levels in central California.

We did not find a consistent relationship between relative abundance of stage I zoeae in the Gulf of the Farallones and subsequent relative abundance of megalopae of the same year class. Therefore, survival or displacement during zoeal stages and early megalopal development apparently are "critical" to the strength of a year class of juvenile crabs. The sampling procedures did not allow us to define more precisely which early life stages are the most critical.

Chapter 7

INTERMOLT STAGING AND DISTRIBUTION OF DUNGENESS CRAB, *CANCER MAGISTER*, MEGALOPAE

by

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INTRODUCTION

The megalopal stage, last and longest of the Dungeness crab, *Cancer magister*, larval stages, is estimated to be in the water column 25 to 30 days before molting to the first juvenile instar (Reilly, Chapter 6). Generally, the zoeal stages become progressively more dispersed and distributed offshore as they develop and eventually disappear from the nearshore area. Molting of stage V zoeae to megalopae occurs offshore and megalopae then appear close inshore in relatively large numbers (Reilly, Chapter 6). Tagging studies show little movement of adult crabs from one fishing area to another (Tasto, Chapter 4) and recruitment to coastal crab populations presumably is related to the number of megalopae which arrive in an area in the plankton and then settle out.

The purpose of my study was to determine the sequence of epidermal changes occurring during the intermolt period between molt of the fifth zoea to megalopa and the molt of megalopa to first juvenile instar, and to use this information to study relationships between the spatial distribution of megalopae and timing of events for this stage.

Descriptions of intermolt stages have been published for a wide range of crustaceans from the primitive and lightly calcified notostracans to the very highly calcified brachyurans. Drach (1939), working with the adult European edible crab, *Cancer pagurus*, first distinguished stages based on integumentary changes and subsequently modified this scheme to include work on less highly calcified taxa (Drach and Tchernigovtzeff 1967). Partitioning the intermolt period into these developmental intervals has made comparisons between crustacean taxa possible (Reaka 1975; Drach and Tchernigovtzeff 1967; Passano 1960; and Stevenson et al. 1968) and has provided a basis for comparing behavioral, chemical, and other structural cyclic changes (Dall and Barclay 1979; Passano 1960; Reaka 1975; Aiken 1973; Stevenson et al. 1968; Tamm and Cobb 1978; and Scheer 1960). A few studies have related intermolt stages more directly to ecological questions. Aiken (1973) studied the relationship of temperature, oogenesis, and size of the American lobster, *Homarus americanus*, to the length of its premolt stages. Davis et al. (1973) statistically analyzed the intermolt cycle in a population of the barnacle *Balanus amphitrite* held in the laboratory. Scheer (1960) estimated duration of intermolt stages of the shrimp *Leander xiphioides* in the field for both winter and spring months. My study on the Dungeness crab is the first description of larval intermolt stages and the first use of this technique for a distributional study.

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MATERIALS AND METHODS

Determination of Intermolt Events

The sequence and duration of intermolt events were determined for a group of Dungeness crab megalopae reared at the Department's Marine Culture Laboratory near Monterey, California. These were the progeny of two females; one collected near Eureka (Figure 18) in June 1977, and the other taken in the Gulf of the Farallones (Figure 11) near San Francisco in May 1977. The females were held in 20-gal (76-liter) aquaria in the laboratory in 10 C seawater. One spawned in late October and the other in early November. Hatching occurred approximately 3.5 months later in February. The zoeae were reared in batch cultures held at about 17 C and were fed live brine shrimp, *Artemia salina*, nauplii. As megalopae appeared, they were transferred once per day to a rotating "care-o-cell" system (Van Olst et al. 1976; Yamada 1977), two each to 5.1-cm (2-inch) diameter cells. Seawater pumped from the ocean nearby was filtered and ultraviolet-treated at the laboratory and then supplied to the cultures in a non-recirculating system. Seawater temperature in the "care-o-cell" system was consistently 1 to 2 C lower than in the zoeal cultures. To minimize temperature shock to the megalopae, the temperature of the transferring water was gradually lowered over a period of about 2 hr to match the "care-o-cell" system. Rearing-water temperatures cycled as ambient temperatures cooled at night and warmed in the afternoon. Incoming seawater also warmed gradually through the megalopal rearing period. Temperatures in the system ranged from 13 to 17.5 C, with an average of 14.7 C.

Megalopae were fed live adult brine shrimp. The cells were cleaned daily of dead food remains and dead megalopae. Enough live brine shrimp were then added to each cell to bring the number to at least 30.

Five to six live megalopae were removed and preserved in buffered 10% seawater formalin each day of the rearing period for intermolt analysis. The second maxillipeds proved to be the best appendages for observing the entire sequence of intermolt events. They are transparent and have large marginal setae, allowing integumentary changes and setagenesis to be seen easily. They were removed under a dissecting microscope and mounted in 50% glycerine under coverslips. This preserved the necessary internal structure for at least the length of this study.

Intermolt stages were identified and length of stage data were obtained. The relative proportion of animals found at each stage was calculated and used, following Scheer (1960), as a measure of average duration of the stage. The assumption is that the distribution of intermolt stages of those individuals which die is similar to those which remain, so that there is no bias due to selective mortality in any one or more of the stages.

Field Distribution Study

The megalopae analyzed for the distributional study came from the Department's Dungeness Crab Research Program sampling during 1976 to 1979 and California Cooperative Fisheries Investigations (CalCOFI) samples from 1949 to 1975 (Figure 27). The extensive nearshore sampling effort of the Dungeness Crab Research Program provided megalopae from oblique and surface plankton

hauls, dipnetting under night-light, dipnetting from nearshore surface waters, and fish stomach contents. CalCOFI cruises provided samples from a large area offshore of the central California coast. Collection methods are described in detail by Reilly (Chapter 6). With few exceptions, intermolt stages of megalopae were discerned easily.

RESULTS

Intermolt Stages

The general format of intermolt staging in the megalopal maxilliped (Table 13; Figure 37) follows that of other crustaceans. After ecdysis the exoskeleton is thin and soft, becoming less deformable as layers of the exoskeleton thicken. A period with no discernible morphological change ensues. The outline of new cuticle then appears and the epidermis pulls away from the old exoskeleton. Seta formation begins at the new cuticle surface and the seta develops as a double structure until it is a "tube within a tube" ready to evert (Figure 37:9-13). At ecdysis the animal withdraws from the old exoskeleton and the setae evert as they are pulled away from the bases of the old setae. I matched my stages with the universal staging of Drach and Tchernigovtzeff (1967) as closely as possible, although a number of observed stages proved difficult. Much of the work on setal changes has been based on observations of septate setae at the margins of crustacean pleopods. The nonseptate setae I observed on the megalopal maxilliped do not form "cones" or septa at the base (Drach and Tchernigovtzeff 1967), nor is progressive stranding and condensation of the setal matrix (Reaka 1975) evident. Many of the megalopal intermolt stages are based on successive measurements of thickening of the exoskeleton at the maxilliped tip, or surrounding the setae. This sequence of events was described in some detail by Davis et al. (1973) in a study of *Balanus amphitrite*. I have relied on this work to help fit my data into Drach and Tchernigovtzeff's (1967) scheme.

Timing

The majority of the megalopae progressed through each of the first four stages quickly and synchronously, while a few lagged behind (Figure 38). Stage five megalopae, however, were found from day 4 until (and beyond) day 27.5, which was the average day of molting to first juvenile instar. It appears that length of this stage not only varied greatly among individuals but was, on the average, the longest stage in this laboratory-reared group. Because of the variability in the length of stage five, it was not possible to measure directly the duration of the succeeding stages. The calculated average duration of stages after stage five indicates, however, that beyond stage five the progression to molting is similar for all megalopae without another highly variable stage. This is also reflected in the progression of time of first appearance of each stage (Figure 38). The appearance of stages 8, 11, and 13 later than the stages which follow is a result of small sample sizes.

Field Distribution of Intermolt Stages

Using the sequence of stages outlined from the intermolt staging study (Figure 37; Table 13), I arranged field-caught megalopae from earliest to latest by sampling location and date.

TABLE 13. Characteristics of Intermolt Stages of Laboratory-reared Dungeness Crab *Megalopae* Based on Observations of the Second Maxilliped.

Maxilliped stage	Universal stage *	Percentage found	Equivalent days	Cumulative days ($\bar{x}$)	Description
1.....	A	0.8	0.2	0.2	Channels left after eversion of the setae are still visible.
2.....	A	6.5	1.8	2.0	Setal matrix fills seta, cuticle thin (1-3 μm), channels no longer visible.
3.....	B	7.3	2.0	4.0	Endocuticle of distal seta and margin between setae thickening (3-7 μm). Matrix of seta still wide at base.
4.....	C	6.4	1.8	5.8	Endocuticle of distal seta very thick (7-8 μm), matrix thin at base.
5.....	D ₀	28.8	7.9	13.7	Separation between epicuticle and epidermis evident as light band (1-3 μm) with membrane.
6.....	D ₀	13.2	3.6	17.3	Outline of tip of new maxilliped below base of distal seta as new layer.
7.....	D ₀	11.5	3.2	20.5	Outline of tip and sides of new maxilliped evident.
8.....	D ₁ '	2.5	0.7	21.2	Short invaginations (< 50% of eventual depth) have formed on either side of the new setal tip.
9.....	D ₁ ''	7.1	1.9	23.1	Invaginations deeper ($\geq$ 50% of eventual depth), but not at maximum depth, no bottom line can be seen.
10.....	D ₁ '''	2.8	0.8	23.9	Distal seta has reached maximum depth, tip still rounded.
11.....	D ₂ '	3.9	1.1	25.0	Tip of distal seta pointed, completely separate from old seta.
12.....	D ₂ ''	7.4	2.0	27.0	Internal shaft of new seta thickening (2-4 μm).
13.....	D ₃	1.8	0.5	27.5	Internal shaft of new seta very thick (4-6 μm).

* Universally accepted intermolt stage nomenclature based on Drach (1939).

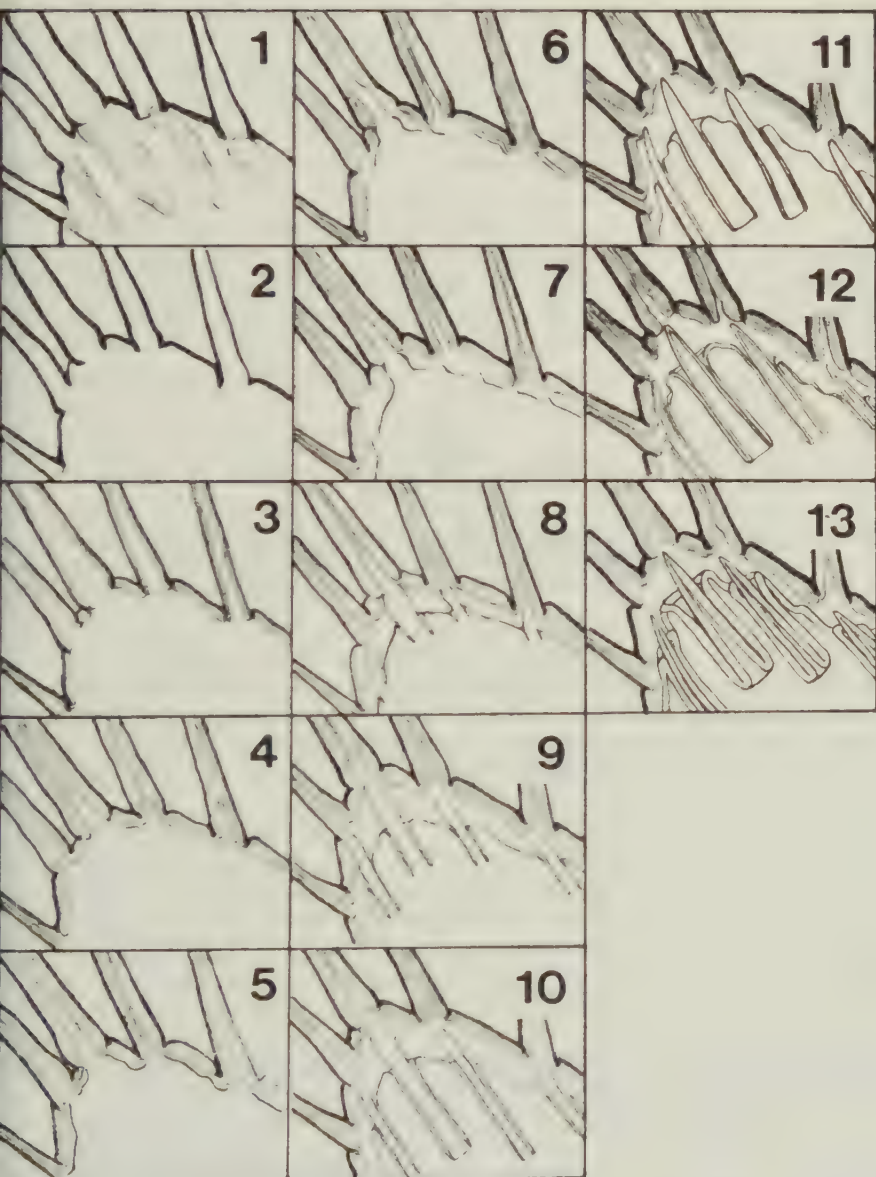


FIGURE 37. Dungeness crab megalopae maxilliped intermolt stages. Smaller setae and tissue detail have been left out to simplify the illustrations.

Offshore

Megalopae from the March 20–29, 1979 cruise and some CalCOFI cruises (1949 to 1975) revealed the only early intermolt stages in my analysis. The first intermolt stage was observed only in megalopae collected from 58 to 193 km offshore. Intermolt stage was negatively correlated with distance from shore

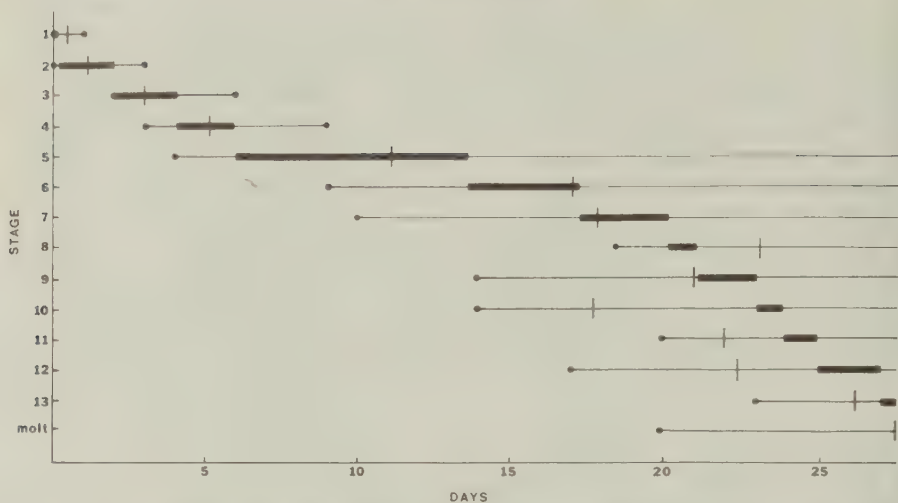


FIGURE 38. Timing of intermolt stages of Dungeness crab megalopae reared in the laboratory. Vertical lines = mean day stage was found; horizontal lines = range; horizontal bars = duration of each stage based on percentage of megalopae found in that stage.

($r = -0.712$), positively correlated with date as month and day ($r = 0.677$), and negatively correlated with latitude ($r = -0.285$). These three variables were compared in a stepwise regression with intermolt stage as the dependent variable. The first variable to enter was distance from shore with a coefficient of determination (r^2) of 0.506. The second variable to enter was latitude which increased r^2 to 0.696, and the third was date for a total r^2 of 0.761. However, distance from shore and date were highly negatively correlated ($r = -0.752$). Thus, the order of entering is not necessarily a good measure of relative importance of the variables. A large proportion of the nearshore samples was taken near San Francisco, which biases the latitude variable to some degree. Some megalopae collected on a CalCOFI cruise in 1960, as far north as Humboldt Bay, were also found close inshore; however, none were later than stage nine. Nevertheless, regression of the three variables, distance from shore, date, and latitude on intermolt stage explains 76% of the variation in the offshore data, and confirms the annual movement of megalopae toward the coast from offshore (Reilly, Chapter 6) over a relatively consistent period of time.

A few more conclusions can be tentatively drawn from the offshore data. The March 6–9, 1950 CalCOFI cruise caught only early stage megalopae (two through five), with 26 found at three stations outside 160 km and only one closer inshore. Megalopae captured during March 23–29, 1979 were also in early stages (one and two), and almost certainly were among the first to molt because so many stage V zoeae were netted during the cruise (Reilly, Chapter 6). These megalopae were distributed from 20 to 148 km offshore. This evidence supports a conclusion that stage V zoeae molted to megalopae 3 weeks to 1 month earlier in 1950 than in 1979, and were possibly farther offshore that year.

Based on the laboratory data, megalopae in stage five were expected to be more numerous in field samples. There is no evidence of a "developmental plateau" or substantially longer stage in the offshore data. The intermolt stages most commonly found were three, six, and seven. The factors which contributed to variability of stage five in the laboratory may be due to the laboratory-rearing situation.

Nearshore

Plankton tows taken nearshore by the Dungeness Crab Research Program in 1977 and 1979 yielded sufficient numbers of megalopae to analyze for intermolt stage distribution. Intermolt stages of these megalopae show definite distributional patterns in both years, as indicated by contour lines (Figures 39 and 40).



FIGURE 39. Frequency distributions and means of Dungeness crab megalopal intermolt stages 6 through 13 at stations in the Gulf of the Farallones and San Francisco Bay, April 1977. Densities from both an oblique and surface tow are summed at each station.

On the April 6–11, 1977 cruise, megalopae in San Francisco Bay, just outside the mouth of the Bay, and in Drakes Bay were developmentally the oldest. The only megalopae found in stage 13 (the last stage) came from San Francisco Bay and Drakes Bay. A large group collected southwest of Pt. Reyes was earlier in development. Intermolt stage means at stations just to the north and south of the Farallon Islands are the lowest, indicating that these megalopae were developmentally the youngest in the area. There were so few individuals caught at these stations, however, that they may not represent the population accurately.

There are a number of other differences between the 1977 and 1979 distributions. The smaller number and earlier average stage of megalopae caught in plankton samples near and in Drakes Bay on April 26, 1979 is pronounced. However, night-lighting on the same date and again the following night attracted large swarms of megalopae (estimated at about 100,000 each). Average stages of 50 megalopae dipnetted and preserved each night from these swarms were 11.2 and 11.5, respectively. These means are comparable to the stage mean found there in 1977.

Megalopae taken by plankton tows in San Francisco Bay on April 27, 1979, near the beginning of the cruise, were also less developed than during early April 1977. Two samples taken close to the Golden Gate 9 days later on May 6 were further along in development, with some in stage 13.

Megalopae from inshore stations north of Pt. Reyes also had a very high proportion in stage 13. Although these were collected on May 2 and 3, past the midway point of the cruise, this cannot account for the extreme lateness of average development. The two Bay samples taken on May 6 were much less skewed toward the more mature stages.

Megalopae captured under a nightlight and from *V. velella* in 1979 did not differ substantially in intermolt stages from megalopae caught in plankton tows at the same station.

A series of samples was taken from a swarm of megalopae at Shaw's Marina in Bodega Harbor at the northern end of Bodega Bay and was analyzed for intermolt stages. A sample taken on April 25, 1979, held in a bucket overnight and preserved the next morning, had 30% stage 13's distributed unevenly from top to bottom; 22% of these were swimming at the top of the bucket and 56% were resting on the bottom. The rest of the sample was predominantly stage 12's with a few 11's. The mean intermolt stage of 50 megalopae dipnetted and preserved on April 26 and 27 was 11.9 for both samples with stage 13's contributing 12% and 18%, respectively. The entire swarm had disappeared from the dock area on April 28.

DISCUSSION

Small-scale patchiness, current patterns, and megalopal behavior may all contribute to the distribution of intermolt stages. All of these including intermolt stages must be considered in analyzing distributions and movement of megalopae in the coastal area near San Francisco and their subsequent settling out. The following is an attempt to present a logically consistent narrative from the available information.

There is evidence from our plankton data that small-scale patchiness is involved in the sampling distribution of Dungeness crab megalopae. A number of stations was occupied both day and night in 1977, and some differences in numbers caught were substantial but without a consistent pattern. There were wide variations in intermolt stages of megalopae at individual stations but, generally, earlier stages were found offshore and later stages inshore.

Before the April 1977 cruise, steady north by northwesterly winds were blowing (Figure 24). During the cruise, upwelling was evident in the cold ($< 9^{\circ}\text{C}$) tongue of water which stretched around and to the south of Pt. Reyes (Figure 21). A Landsat photograph from May 17, 1977 (Figure 41), taken 1 month after the last plankton sample was collected that year, shows a counterclockwise gyre

of surface water from the outer edge of Pt. Reyes into Drakes Bay. This gyre develops during the upwelling season (Pirie and Steller 1977) and is consistent with surface drifter recoveries in March of 1970 and 1971 (Conomos et al. 1971). It is probable that megalopae move into Drakes Bay in this gyre and the same population, in fact, may have been sampled in Drakes Bay on April 9, 1977 as had been sampled outside Pt. Reyes on April 6, 1977. The mean intermolt stage in Drakes Bay was about 1.5 stages later than those outside Pt. Reyes, a reasonable 3-day difference (Figure 38). The approximately 40- to 80-km gyre could be covered in 3 days if an average speed of 15 to 31 cm/sec was maintained. Current meters off the Oregon coast have measured rates of southward flow at 40 cm/sec at a depth of 5 m during upwelling (Halpern 1976), so these speeds are reasonable. Concentration of megalopae by the gyre probably explains the large number of early post-larval crabs which were found 1 month later in Drakes Bay (Tasto, Chapter 10).

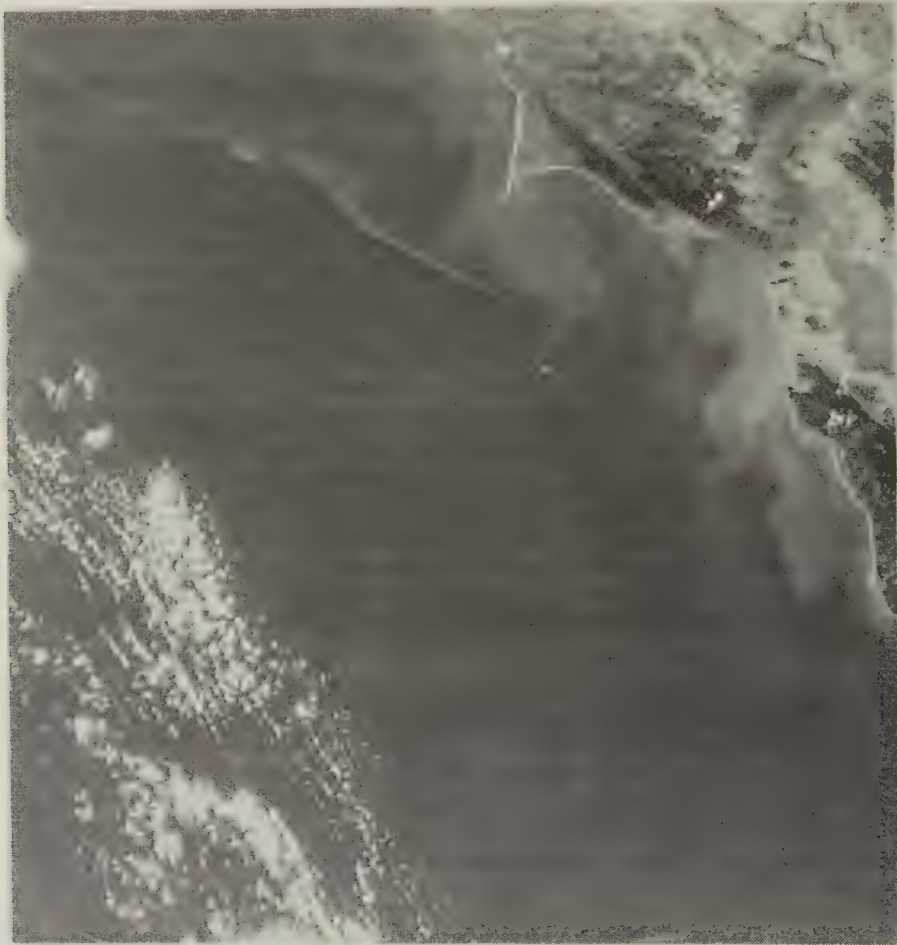


FIGURE 41. Satellite (Landsat) photograph of study area taken May 17, 1977.

During the 1979 cruise, upwelling apparently was not as strong as in 1977. Northwesterly winds had ceased temporarily by April 21 and were replaced by a series of days with variable winds (Figure 24) and the tongue of cool water reaching into the Gulf of the Farallones was 1 to 2 C warmer than in 1977 and more stratified.

A large group of megalopae evidently had moved into the nearshore area in 1979 before the cruise began on April 24. The great number attracted by night-light in Drakes Bay on April 24 and 25 supports this conclusion. Also, a large swarm of megalopae appeared at the surface in Shaw's Marina on April 25 and a large number had been seen at Mason's Marina, closer to the ocean in Bodega Harbor on April 20. Large numbers were taken north of Pt. Reyes on May 2 and 3 (Figure 40). However, few megalopae were taken in plankton tows in Drakes Bay and most other Gulf stations on this cruise.

All of the megalopae collected along the coast north of Pt. Reyes in May 1979 were in late stages. Approximately 59% were stage 13's and about 10% of these had a thick layer of diatoms covering parts of their exoskeleton. If these are simply the remainder of the large influx that moved inshore before our cruise began, and no more earlier stages were moving into this area, this may account for the extreme lateness of stage. However, other nearshore areas where megalopae were settling out had a much smaller percentage of stage 13's. This suggests that conditions for the megalopae north of Pt. Reyes may not have been conducive to settling, and that they probably had been at the surface longer than usual to provide enough light for algal growth. Perhaps currents were keeping them from settling. It may be that megalopae will not molt unless they are in contact with a substrate long enough to accomplish a molt. "Developmental plateaus" are well known for adult crustaceans (Reaka 1975) but usually occur during mid-intermolt rather than late-intermolt. However, if megalopae are unable to settle on a substrate, the ability to delay molting would be advantageous. An effort to test this in the laboratory by directing a water current to keep a late-stage megalopa away from any surfaces failed when the megalopa was able to cling to screening and molt.

The majority of megalopae appeared to be dropping down some time during stage 12. Most of the megalopae found in bottomfish stomachs were in intermolt stages 12 and 13, although there were some exceptions. It is puzzling that no megalopae could be dipnetted from near the bottom at Shaw's Marina when there were so many in late stages at the surface. Jim Houk (Calif. Dep. Fish and Game, pers. commun.) noted that a group of megalopae held over a sand bed in the laboratory buried into the sand with only their eyes protruding a few days before molting to the first juvenile instar. If this is normal behavior in the wild, it would help to explain their absence from the Shaw's Marina water samples near the bottom. The fact that there are stage 13's in the water column in Bodega Bay, Drakes Bay, and San Francisco Bay, may mean that burying in the substrate is not a consistent pre-molt behavior or that a suitable substrate in which to bury cannot always be found. Observations of field-collected and laboratory-reared megalopae show that burying in sand is not a necessary requirement for molting.

Presumably, the megalopae in Shaw's Marina had all settled out by April 28. This is consistent with night-lighting results in Drakes Bay, where on April 30 and May 1 no megalopae were attracted by the night-light and those which had been collected there on April 26 and 27 began molting to the juvenile instar overnight.

Areas with concentrations of juvenile crabs (Tasto, Chapter 9) are located where currents are likely to concentrate megalopae until they are ready to settle. In Drakes Bay and Bodega Bay, eddies presumably deposit megalopae in areas without great current flows, allowing them to remain and eventually drop down to the bottom. It is possible that variable winds and relaxation of upwelling in 1979 diverted northward some megalopae which would normally have entered the Gulf around Pt. Reyes, helping to account for the large numbers found off Pt. Reyes Beach that year.

In all, 97 megalopae were collected in San Francisco Bay plankton samples with intermolt stages ranging from 8 to 13. Four of these were collected at the surface and the remainder were taken in oblique tows. Only the latest stages would be expected in the Bay if megalopae only moved in with prevailing bottom currents (Conomos et al. 1971) after settling to the bottom near the Golden Gate. Because not all were in the latest stages, it may be that inward-moving sub-surface currents influence most of the water column, that tidal currents carry some in, or that most megalopae are closer to the bottom, regardless of maturity, in this area where surface salinity is lower than the Gulf.

Intermolt staging has allowed some elucidation of megalopal movement patterns and factors resulting in megalopal concentrations in the nearshore area. My analysis confirms the movement of megalopae from offshore to inshore. However, because surface transport is directed primarily offshore when the megalopae appear inshore, it is not yet clear how megalopae move from offshore to inshore; nevertheless, our studies did not reveal movement of Dungeness crab megalopae away from the nearshore area. A number of variables appear to be involved in nearshore megalopal distribution patterns but currents emerge as the most influential. Nearshore current patterns, such as gyres, during the megalopal period appear to depend on the establishment of upwelling and would be expected to be relatively consistent by the time the megalopae are close to shore. These nearshore current patterns, as well as changes in currents during periods of southerly or variable winds, appear to influence the specific areas of concentration.

Chapter 8

DISTRIBUTION OF ZOOPLANKTON IN ASSOCIATION WITH DUNGENESS CRAB, *CANCER MAGISTER*, LARVAE IN CALIFORNIA

by

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INTRODUCTION

There has been little investigation of relationships between the zooplankton community and the nearshore ocean current system of the central California Coast. Dungeness crab, *Cancer magister*, larvae are members of this community primarily from the time they hatch in late December-mid-January until they settle out to metamorphose to the juvenile stage in early April-early May. In an effort to explore the influences of ocean currents on Dungeness crab larvae, I analyzed distributions and abundance of both holoplankton and meroplankton in the Gulf of the Farallones off San Francisco (Figure 11) and northward along the California coast to infer water mass movements and locations of entrapment zones.

Relating species populations with specific water masses has been both the object and result of much marine and estuarine zooplankton work. A few examples are listed here. Russell (1935 and 1936) used zooplankton as indicators of water movement in the English Channel and the North Sea. Fraser (1952) used chaetognaths and other zooplankton to trace movements and dispersal of water of various origins near Scotland. Bieri (1959) related chaetognath distributions throughout the Pacific Ocean to defined water masses. Seasonal and offshore-onshore trends in composition, distribution, and abundance of New York Bight zooplankton yielded information on seasonal intrusion of the Gulf Stream and advection of cold-water species from the northeast (Judkins et al. 1980).

Work in the upwelling zone off Oregon revealed relationships between strength of upwelling and zooplankton species composition and abundance (Peterson and Miller 1975). Studies in the same area on distributions of life stages of common nearshore copepods were used to define dynamics of upwelling including a divergent frontal region, thickness and extent of the offshore moving Ekman layer, and dynamics of relaxation periods (Peterson et al. 1979). These latter two references are directly applicable to my analysis because of proximity, similarity of species composition, and seasons sampled.

Some information on zooplankton of the northern and central California coast is available in publications of California Cooperative Fisheries Investigations (CalCOFI), La Jolla, California. These data, however, are based on a sampling

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program with relatively few cruises reaching as far north as San Francisco and even fewer as far as Cape Mendocino (Figure 27). While there is this limited information about zooplankton of central and northern California, the zooplankton of the Gulf of the Farallones (Figure 11) was virtually unknown when our study began.

MATERIALS AND METHODS

The zooplankton samples I analyzed were collected during spring 1976, winter and spring 1977, and March 1979 (Reilly, Chapter 6). The 1976 and 1977 cruises covered the Gulf of the Farallones and the 1979 cruise extended from the Gulf north to Cape Mendocino. In 1976 and 1977, 505- μ m mesh plankton nets were used, and in 1979, a 1.0-mm mesh net was used. Only oblique plankton tow samples were used in this analysis.

In the laboratory, settled volumes of the samples were measured and samples were diluted for species counts. Stempel piston pipette aliquots (2 ml) were used to estimate abundance for the samples taken with the 505- μ m mesh net. Rare species were counted in up to five 2-ml aliquots to obtain a more accurate estimate of abundance. Larger zooplankters such as the salp *Salpa fusiformis* and heteropod *Carinaria japonica* were removed before aliquoting and counted separately for the entire sample. For the rarer species an attempt was made to reach a count of more than 10 individuals, or for the rarest species, to count all individuals in five 2-ml aliquots. Very large samples were split with a Folsom splitter to a workable size (usually $\frac{1}{4}$ or $\frac{1}{8}$ of the total) before subsampling.

The March 1979 samples usually were split to $\frac{1}{8}$ or $\frac{1}{16}$ for the first count of all species. The overall larger size of organisms caught with the 1.0-mm mesh net made use of the piston pipette for subsampling too inaccurate. The counting procedure for the remaining fractions was similar to the aliquoting routine with the more abundant species dropped out of the counting as each larger fraction of the sample was inspected.

Zooplankters were identified to the lowest taxon possible. An effort was made to maintain continuity and uniformity in taxonomy despite several changes in personnel. However, some zooplankton identified to species in 1977 were only identified to family or above in 1976 and comparisons in occurrences by year cannot be made for these taxa.

Approximately 152 zooplankters and (or) various stages of zooplankters were identified. Of these, 130 were chosen for analysis. Only those which were very rare were left out. A complete list of the zooplankters identified is available in Tasto et al. (1981).

All oblique tow data for 1976 and 1977 were analyzed using the recurrent group analysis method of Fager (1957) and Fager and McGowan (1963). These 2 years were analyzed separately to compare between years. This was important because the Dungeness crab reproductive cycle is repeated annually and we only sampled during spring in 1976. The recurrent group analysis method uses presence and absence data to determine groups having the largest numbers of species with affinities for each other. Fager and McGowan developed an index of affinity for this purpose. They considered that species should be found together in somewhat more than half of the recorded occurrences (their index value of 0.5 or above) if they were to be grouped together. I also used an index of 0.5 and above to show affinity. The number of species affinities between

groups is a measure of how closely groups are allied.

While this gave a general overview of species co-occurrence, more detailed information on distribution and abundance was needed. With the aid of computer analysis, maps of distribution and abundance of the more common species were prepared for three cruises in 1976 and three in 1977 (76301, 76507, 76508; 77102, 77105, 77503; Appendices IV and V). These six cruises were chosen because they covered the entire Gulf and included a large portion of the data.

I considered the data from the March 16–31, 1979 cruise less suitable for recurrent group analysis because the majority of the stations were in three widely separated sets of transects (Figure 16). For these data, abundance of species at each station was arrayed in a matrix of latitude versus distance from shore. Mann-Whitney U-tests were used to test equality of abundance for Cape Mendocino transects versus Gulf of the Farallones transects, and day versus night tows for all transects.

RESULTS

Results from 1977 are reported first and in more detail than 1976 because a larger number of samples was taken over a broader period of time and a larger proportion of the species were identified to lower taxa. The less complete 1976 results for the Gulf of the Farallones are then reported and compared to 1977. The 1979 results are reported last.

Gulf of the Farallones

1977

Recurrent group analysis of the oblique tows taken in 1977 revealed 13 groupings (Table 14; Figure 42). Three of these groups (6, 12, and 13) each had so few occurrences (< 10) that they are not included nor discussed further.

Group 1 contains species or families which occurred consistently throughout the entire Gulf of the Farallones or throughout the nearshore half. This group can be divided into two subgroups, (i) larvae of nearshore bottom-dwelling decapods, a copepod *Acartia clausi*, and a ctenophore *Pleurobrachia bachei*, all of which were highest in abundance at the most inshore stations; and (ii) other holoplanktonic species which were highest in abundance farther from shore. Although these two subgroups have different patterns of distribution and abundance, they were both found so consistently in a large portion of the samples taken in the Gulf in 1977 that they grouped together.

Some differences between cruises are evident, however. Most of the decapod larvae in Group 1 were distributed throughout the Gulf in the January cruise but were found only in the inner half on later cruises. Exceptions were the crab larvae *Cancer productus* zoeae I–III, majid zoea I, and majid zoea II which were found throughout the Gulf on all three mapped cruises, although occurring more sporadically at the outermost stations in the later two cruises. Most species within this subgroup were consistently highest in abundance inshore for all three mapped cruises. However, *Callinassa* (ghost shrimp) larvae, pagurid (hermit crab) larvae, and *Cancer gracilis* zoeae II–III were highest in abundance farther from shore during the January cruise, and densest inshore later (Figures 43 and 44; Table 14). This was also true of *P. bachei* and *A. clausi*.

TABLE 14. Recurrent Grouping, Occurrence, General Distribution, and Maximum Abundance of Gulf of the Farallones Zooplankton from Oblique Tows Taken in 1977.

Species	Group	Occurrences* (out of 159)	Distribution ¹ and maximum abundance (no./m ³)* by cruise and date		
			77102 1/27-2/3	77105 4/6-4/11	77503 5/9-5/21
<i>Pleurobrachia bachei</i>	1	66	O 1.40	I 4.89	I 4.56
<i>Acartia clausi</i>	1	126	I 5.23	I 28.62	I 73.06
<i>Calanus pacificus</i>	1	134	O 32.46	M 84.46	M 412.69
<i>Calanus tenuicornis</i>	1	106	M 3.28	M 15.61	M 44.10
<i>Metridia lucens</i>	1	97	M 9.60	M 93.40	O 51.59
<i>Callinassa</i> larvae	1	104	M 20.19	I 32.98	I 1.85
<i>Pagurid</i> larvae	1	96	M 4.88	I 7.33	I 1.19
<i>Cancer productus</i> zoeae I-III	1	134	I 1.75	I 3.81	I 2.56
<i>Cancer antennarius</i> zoeae II-III	1	110	I 20.23	I 86.25	I 12.19
<i>Cancer antennarius</i> zoeae IV-V	1	89	I 2.86	I 20.08	I 22.04
<i>Cancer gracilis</i> zoeae II-III	1	68	M 2.74	I 7.92	I 0.64
<i>Pinnotherid</i> zoeae I-III	1	119	I 85.02	I 89.69	I 7.32
<i>Pinnotherid</i> zoeae IV-V	1	90	I 4.49	I 43.59	M 228.30
<i>Majid</i> zoea I	1	115	I 3.12	I 2.20	M 0.17
<i>Majid</i> zoea II	1	96	M 1.57	I 1.35	M 0.07
<i>Sagitta euneritica</i>	1	101	M 6.64	I 7.33	M 1.73
<i>Tomopteris septentrionalis</i>	2	52	O 0.23	O 1.04	O 0.10
<i>Eucalanus bungii</i>	2	88	O 3.93	O 7.40	O 3.48
<i>Neocalanus cristatus/plumchrus</i> ⁵	2	32	-	O 3.62	O 1.21
<i>Euchirella rostrata</i>	2	53	M 1.45	M 3.66	(O 0.01) ¹¹
<i>Heterorhabdus papilliger</i>	2	29	O 1.83	M 10.99	(O 0.48)
<i>Thysanoessa spinifera</i>	2	38	(O 0.61)	M 0.94	O 2.50
<i>Doliolotta gegenbauri</i> old nurse ¹¹	2	28	O 0.05	M 0.15	(M 0.02)
<i>Sagitta scrippsae</i>	2	48	(O 0.20)	M 0.88	M 0.71
<i>Sagitta decipiens</i>	2	55	(O 0.32)	M 4.88	O 1.94
<i>Eukrohnia hamata</i>	2	21	-	M 0.64	(M 0.02)
<i>Liriope tetraphylla</i>	3	27	O 13.56	-	-
<i>Atlanta peroni</i>	3	16	O 0.78	-	-

<i>Evadne</i> sp.	3	26	1	4.19	(M 0.01)	(M 0.01)
<i>Candacia bipinnata</i>	3	28	O	3.66	-	-
Sergestid larvae	3	26	O	5.23	-	(I 3.41)
Echinopluteus	3	12	O	1.74	-	-
Ophiopluteus	3	18	O	2.62	-	-
Brachiopod larva	3	20	M	0.88	-	-
<i>Sagitta enflata</i>	3	34	M	4.66	-	-
<i>Upogebia pugettensis</i> larvae	4	56	I	7.85	I 7.33	I 4.24
Porcellanid larvae	4	49	I	2.18	I 1.35	I 9.89
<i>Cancer antennarius/gracilis</i> zoea I	4	105	I	43.01	I 24.85	I 19.08
Grapsid zoeae I-III	4	71	I	5.67	I 34.06	I 9.78
Grapsid zoeae IV-V	4	39	M	0.25	I 3.41	I 3.74
<i>Cancer antennarius</i> megalopa	5	67	M	0.25	M 0.15	M 5.44
<i>Cancer gracilis</i> zoeae IV-V	5	68	O	2.45	I 0.33	M 0.93
<i>Cancer gracilis</i> megalopa	5	64	M	0.20	M 0.03	M 0.43
Majid megalopa	5	79	M	0.08	M 0.15	M 0.14
<i>Rhinalanus nasutus</i>	7	57	M	10.91	O 0.38	O 0.77
<i>Parathemisto pacifica</i>	7	46	M	0.87	O 0.01	O 0.19
<i>Cancer magister</i> zoea I	7	28	M	0.04	M 0.02	(M 0.02)
<i>Cancer oregonensis</i> zoeae I-III	7	62	I	4.49	M 0.38	(M 0.14)
<i>Limacina helicina</i>	8	40	M	0.88	M 0.74	(M 0.28)
<i>Emerita analoga</i> larvae	8	63	M	0.28	M 0.68	I 0.87
<i>Pseudocalanus</i> sp.	9	53	(O	0.58)	M 14.95	M 129.70
<i>Cancer magister</i> megalopa	9	27	-	-	M 0.10	(M 0.01)
<i>Doliioletta gegenbauri</i>	10	20	O	1.31	(O 0.01)	(O 1.55)
<i>Oikopleura vanhoffeni</i>	10	29	M	14.90	-	M 2.28
<i>Tortanus discaudatus</i>	11	73	I	3.14	I 9.65	M 75.34
Xanthid zoeae I-II	11	74	(M	0.09)	I 2.06	I 2.88

* Includes all 1971 oblique plankton samples.

† Includes only mapped cruises (cruise codes are explained in Appendix III).

O = Offshore: highest abundances offshore, caught at very few inshore stations.

M = Mid-Gulf: highest abundances at mid-Gulf stations, lower abundance both inshore and offshore.

I = Inshore: highest abundances inshore, generally not found beyond mid-Gulf stations.

† Maximum abundance was judged to reflect relative abundance between cruises as well as or better than other measures. It indicates the abundance in areas which often contain most of the total numbers found. Wide variations in abundance throughout the Gulf made average abundance less useful.

‡ Both were identified as *Neocalanus cristatus*.

§ Parentheses indicate two or fewer occurrences.

* The parent oozoid after the blastozoids have detached. Little internal structure and wide muscle bands are characteristic.

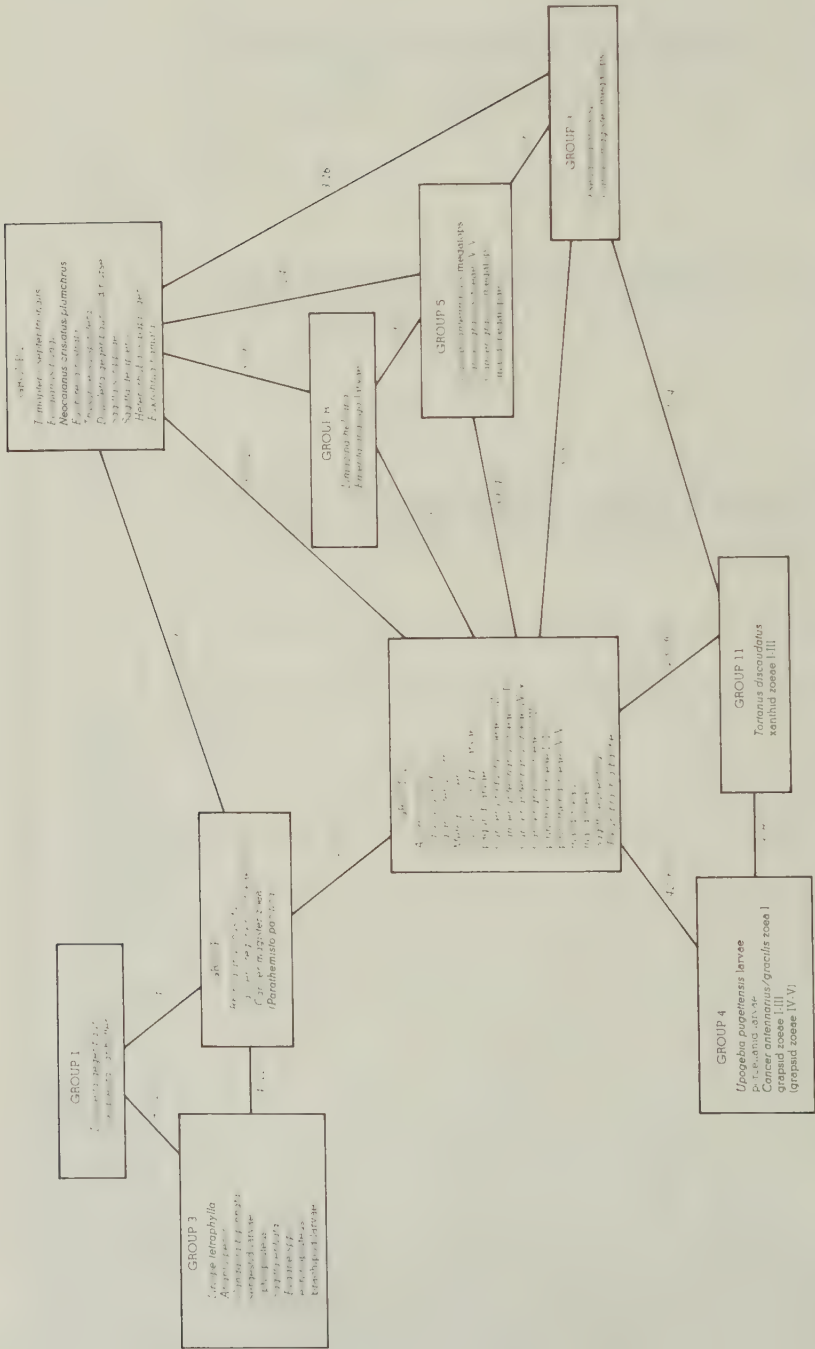


FIGURE 42. Recurrent groups of zooplankters in the Gulf of the Farallones during late winter and spring 1977. Fractions are the number of affinities between groups over the number possible. Forms in parentheses have affinities only within their group, but not with all in the group. They were not used in cross-group affinity ratios.



FIGURE 43. Distribution of *Callinassa* larvae, cruise 77102, January 27 to February 3, 1977.



FIGURE 44. Distribution of *Callinassa* larvae, cruise 77105, April 6 to April 11, 1977.

The highest abundances for those inshore species were in one of two areas or both. These areas were (i) around the San Francisco Bay mouth and (or) extending to the south nearshore, and (ii) at either of two stations in Drake's Bay. Between these two areas, most often at the station nearest Double Point, many of these zooplankters were lower in abundance or absent. This distribution is characteristic of many of the nearshore species as illustrated by the copepod *Tortanus discaudatus* (Figure 45), an inshore species in Group 11.



FIGURE 45. Distribution of *Tortanus discaudatus*, cruise 77102, January 27 to February 3, 1977.

The rest of the species in Group 1 were more abundant in mid- or outer-Gulf, with low abundances inshore. The exact configuration of high density areas varied by species from a large area paralleling the coastline (e.g. the copepod *Calanus pacificus*; Figure 46), to smaller high density areas west or southwest of the San Francisco Bay mouth. With the exception of the copepod *Metridia lucens*, all of the species within Group 1 were also caught in San Francisco Bay during all three cruises.



FIGURE 46. Distribution of *Calanus pacificus*, cruise 77503, May 9 to May 21, 1977.

Group 2 consists of species which generally were distributed more offshore than Group 1. There were, however, as with Group 1, notable differences between cruises. During the January cruise the copepod *Neocalanus cristatus/plumchrus* and a chaetognath *Eukrohnia hamata* were not found in the Gulf while the chaetognaths *Sagitta decipiens* and *Sagitta scrippsae*, an euphausiid *Thysanoessa spinifera*, and a doliolid *Dolioletta gegenbauri* old nurse, were found at just a few stations offshore (e.g. Figure 47). The remainder in Group 2 were common during the January cruise but more abundant at offshore stations. The only occurrences of Group 2 species at the most inshore stations were low numbers of the copepod *Euchirella rostrata* near Double Point and low numbers of the copepod *Eucalanus bungii* at Drake's Bay, Double Point, and Pt. San Pedro (Figure 11).



FIGURE 47. Distribution of *Sagitta scrippsae*, cruise 77102, January 27 to February 3, 1972.

Group 2 species generally were more abundant in April and distributed farther inshore, although they were still low in numbers or absent from Drake's Bay and the area around the San Francisco Bay mouth (e.g. *S. scrippsae*; Figure 48). Exceptions were *D. gegenbauri* old nurse which remained offshore and *T. spinigera* which, although closer in, was less abundant during this cruise. In May Group 2 species were found at fewer stations, in lower abundance, and not as close inshore as in April (Table 14).

Several affinities between Groups 1 and 2 were evident. *E. bungii* occurred throughout much of the Gulf in all three cruises and thus has many affinities with Group 1. Other cross-group affinities occurred between mid-Gulf copepod species in Group 1 and three more commonly occurring species in Group 2, the polychaete *Tomopteris septentrionalis* and chaetognaths *S. scrippsae* and *S. decipiens*.

Group 3 is a major group and quite distinct from all the rest. The only cross-group affinities are with the small Groups 10 and 7. Group 3 is markedly separate because the forms were found almost exclusively during the January cruise (Table 14). Some of these species were higher in abundance at the



FIGURE 48. Distribution of *Sagitta scrippsae*, cruise 77105, April 6 to April 11, 1977.

offshore edge of the Gulf (e.g. the copepod *Candacia bipinnata*; Figure 49) while others, such as the chaetognath *Sagitta enflata*, occurred throughout the Gulf with higher abundances mid-Gulf. The only form found in San Francisco Bay was a cladoceran *Evadne* sp.

The forms comprising Group 4 were found only close inshore. Many of these forms have affinities with Group 1. The only cross-group affinities missing are those with the more offshore species of Group 1 (*Calanus tenuicornis*, *Metridia lucens*, and *Sagitta euneritica*). Distribution and abundance patterns of the members of this group are similar throughout all three cruises. Higher densities were found in Drake's Bay, particularly the eastward station, and around and to the south of the San Francisco Bay mouth. There is some evidence of movement offshore during the January cruise; both grapsid crab zoeae IV-V and *Cancer antennarius/gracilis* zoea I (*C. antennarius* and *C. gracilis* zoea I are indistinguishable at this stage) were sporadically found to mid-Gulf during this cruise, but were only found close inshore during later cruises. With the exception of grapsid zoeae IV-V, all forms in Group 4 also were consistently found in San Francisco Bay.

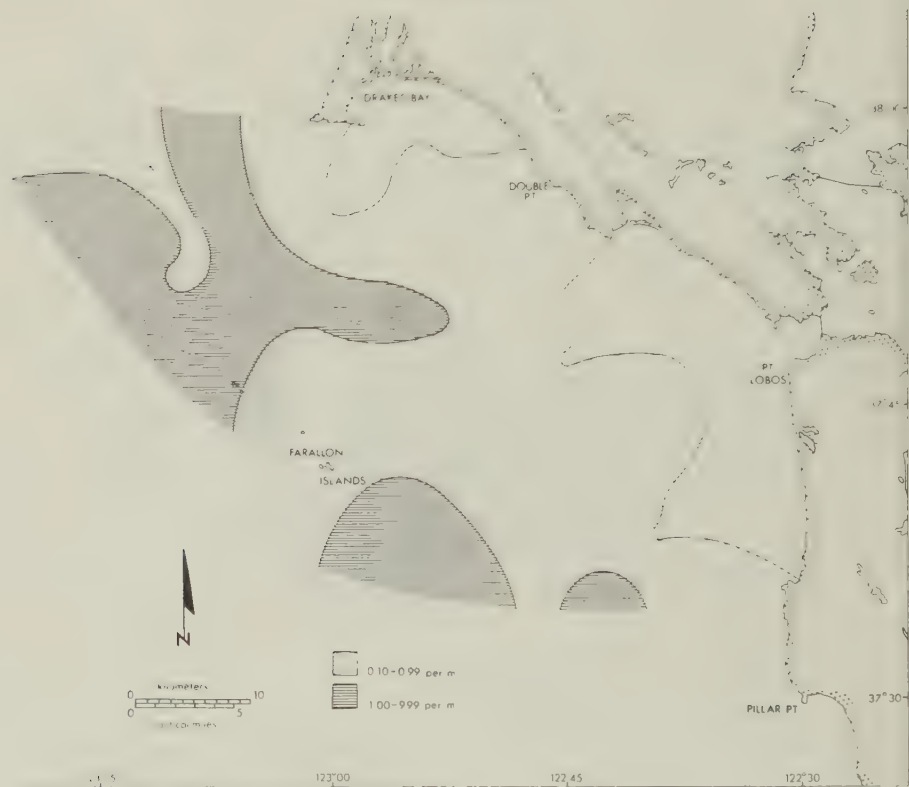


FIGURE 49. Distribution of *Candacia bipinnata*, cruise 77102, January 27 to February 3, 1977.

Group 5 consisted of three species of crabs, all in late larval stages (Table 14; Figure 42). This group is closely allied with Group 1, having affinities with all but those closest inshore. This group showed a pattern of seasonal changes similar to Group 1, with higher abundances farther offshore in January and closer toward shore in April and May. Group 5 is also linked with Group 2 through affinities with the copepods *Eucalanus bungii* and *Euchirella rostrata* which were found throughout most of the Gulf.

Group 7 included four species, a copepod *Rhincalanus nasutus*, *Cancer oregonensis* zoeae I-III, *Cancer magister* zoea I, and a hyperiid amphipod *Parathemisto pacifica*. *R. nasutus* has affinities with Group 3 and was found throughout most of the Gulf during the January cruise, although it was grouped with *C. oregonensis* zoeae I-III in Group 7 because both also appeared in late cruises. While both of these species show similarities in timing of their occurrence, *R. nasutus* characteristically was found only offshore or higher in abundance offshore during all three cruises (Figures 50 and 51). *C. oregonensis* zoeae I-III, in contrast, were densest inshore during the January cruise and near Drake's Bay in April. They were captured at only one mid-Gulf station in May. Both *R. nasutus* and *P. pacifica* were captured in San Francisco Bay in January. The majority of cross-group affinities between Groups 7 and 1 are due to links with *C. oregonensis* zoeae I-III. The only affinity for *C. magister* zoea I was with this

same form. This is not surprising because these two are the only forms which appeared predominately in January, became scarce in April, and were rare in May. *C. magister* zoea I was much less abundant than *C. oregonensis* zoeae I-III, however, and rarely appeared close inshore.



FIGURE 50. Distribution of *Rhinocalanus nasutus*, cruise 77102, January 27 to February 3, 1977.

The two species in Group 8 have no obvious characteristics tying them together. The pteropod *Limacina helicina* has distributional characteristics of many of the more offshore species in Group 2, and was found inshore only near Double Point (Figure 52). Sand crab, *Emerita analoga*, larvae account for most of the affinities with Group 1, but the distributional pattern does not fall into any of the categories described above.

Group 9 consists of *C. magister* megalopae and the copepod *Pseudocalanus* sp. *Pseudocalanus* was very low in abundance in January but more abundant later in the year. *C. magister* megalopae were not found in the Gulf during January, but appeared in April throughout much of the Gulf. Only a few were caught in May. Affinity between these two forms can be traced to their paucity during January and greater numbers later in the year. The only other affinity for *C. magister* megalopae is with *Sagitta decipiens*, apparently for the same reasons.



FIGURE 51. Distribution of *Rhincalanus nasutus*, cruise 77105, April 6 to April 11, 1977.

The two species comprising Group 10, *Dolioletta gegenbauri* and the larvacean *Oikopleura vanhoffeni*, were caught in the Gulf during the January cruise and, except for one *D. gegenbauri*, were not caught in April. They re-appeared again during the May cruise. *D. gegenbauri* was found in the outer half of the Gulf in January, and only at a few outer stations (although in substantial numbers) in May. *O. vanhoffeni*, in contrast, was found throughout much of the Gulf, with highest abundances mid-Gulf and in low numbers inshore (Table 14). Both of these species have cross-group affinities with most of Group 3.

The two species in Group 11, *Tortanus discaudatus* and xanthid crab zoeae I-II were allied with Groups 1 and 4; however, both were found less often and in lower abundances during the January cruise. This appears to account for their grouping separately despite their being in nearshore to mid-Gulf ranges of both Groups 1 and 4. *T. discaudatus* was most abundant in May in mid-Gulf, west of the Golden Gate. Earlier it was in higher abundance nearshore both in Drake's Bay and around the San Francisco Bay mouth. Xanthid zoeae I-II were most abundant at the closest inshore stations on the two later cruises.

1976

Recurrent group analysis of the 1976 zooplankton data revealed three separate groups (Figure 53; Table 15). The distributional patterns did not change markedly from cruise to cruise in 1976. All of these cruises were during the spring upwelling season, so this result was not unexpected. There was the same overall inshore-offshore group separation which was characteristic of the two spring 1977 cruises.

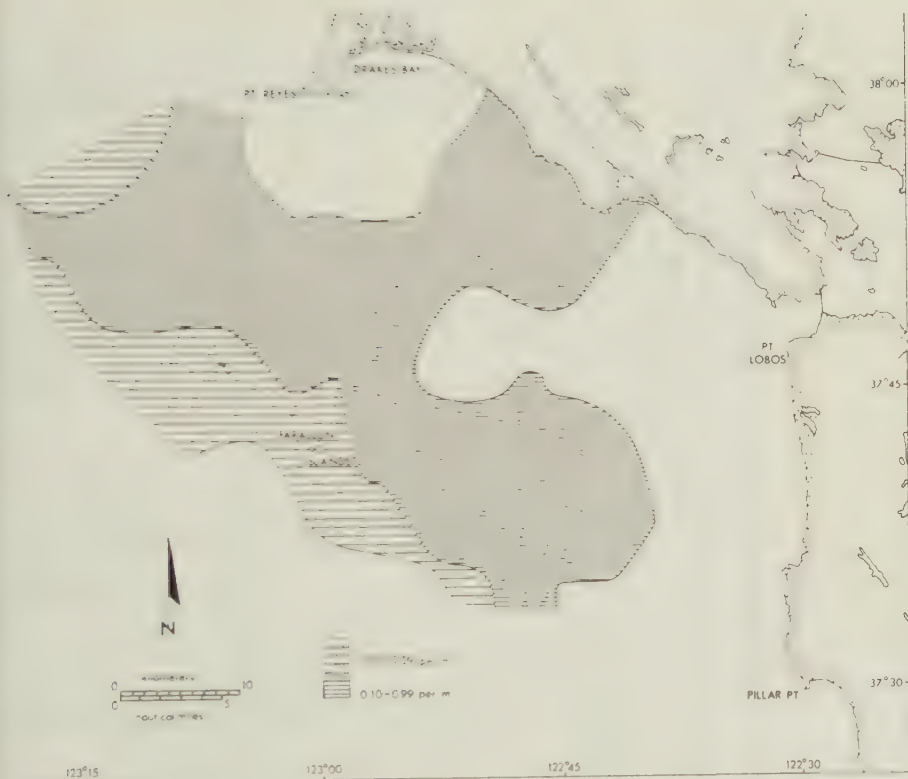


FIGURE 52. Distribution of *Limacina helicina*, cruise 77102, January 27 to February 3, 1977.

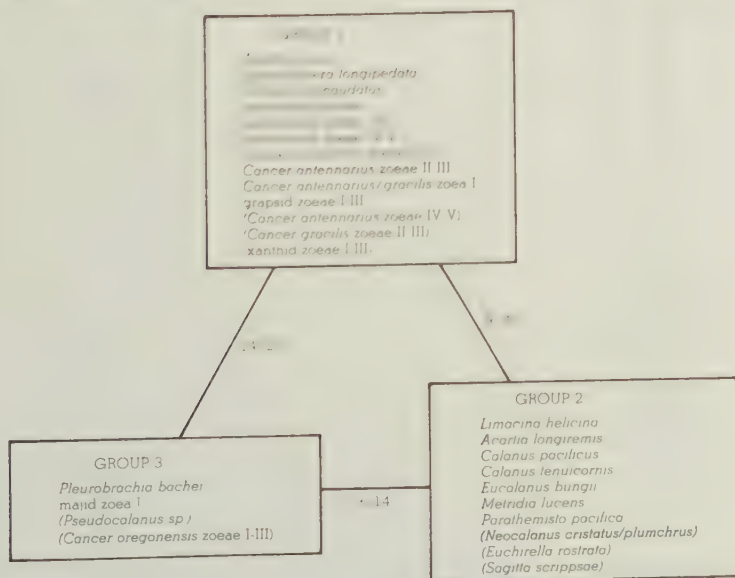


FIGURE 53. Recurrent groups of zooplankters in the Gulf of the Farallones during spring 1976. See Figure 42 for explanation.

TABLE 15. Recurrent Grouping, Occurrence, General Distribution, and Maximum Abundance of Gulf of the Farallones Zooplankton from Oblique Tows Taken in 1976.

Species	Group	Occurrences* (out of 89)	Distribution† and maximum abundance (no./m ³)‡ by cruise and date		
			76301 3/18-3/31	76507 4/24-5/4	76508 5/24-6/5
<i>Acartia clausi</i>	1	44	I 292.70	I 26.85	I 2.20
<i>Epilabidocera longipedata</i>	1	43	I 50.55	I 3.85	I 6.60
<i>Tortanus discaudatus</i>	1	65	M 364.80	M 64.94	M 119.86
Porcellanid larvae.....	1	30	I 6.59	I 7.94	I 1.46
Pinnotherid zoeae I-III.....	1	57	I 342.86	I 10.96	I 9.90
Pinnotherid zoeae IV-V.....	1	57	I 125.27	I 4.58	I 11.33
<i>Cancer productus</i> zoeae I-III.....	1	49	I 0.66	I 0.55	I 0.36
<i>Cancer antennarius</i> zoeae II-III.....	1	45	I 46.42	I 5.60	I 110.46
<i>Cancer antennarius</i> zoeae IV-V.....	1	31	I 2.55	I 0.25	I 17.26
<i>Cancer gracilis</i> zoeae II-III.....	1	27	I 2.09	I 0.16	(I 0.08)§
<i>Cancer antennarius/gracilis</i> zoea I.....	1	45	I 11.25	I 13.50	I 27.62
Grapsid zoeae I-III.....	1	30	I 13.01	I 2.20	I 3.46
Xanthid zoeae I-II.....	1	28	M 0.22	I 0.49	I 3.46
<i>Limacina helicina</i>	2	46	O 4.67	M 0.86	O 0.55
<i>Acartia longiremis</i>	2	45	O 2.47	M 5.98	M 6.60
<i>Neocalanus cristatus/plumchrus</i> II.....	2	25	O 2.47	O 0.46	O 0.18
<i>Calanus pacificus</i>	2	74	M 39.60	M 3.57	M 116.05
<i>Calanus tenuicornis</i>	2	32	M 1.31	M 0.41	O 1.10
<i>Eucalanus bungii</i>	2	47	O 6.04	O 2.20	O 3.30
<i>Euchirella rostrata</i>	2	18	M 1.31	(O 0.01)	-
<i>Metridia lucens</i>	2	54	M 43.00	M 10.76	O 75.90
<i>Sagitta scrippsae</i>	2	19	N.I.†	O 0.11	O 0.18

<i>Pleurobrachia bachei</i>	3	49	I	2.60	I	3.56	I	0.73
<i>Pseudocalanus</i> sp.	3	54	M	5.22	M	44.66	M	6.85
<i>Cancer oregonensis</i> zoeae I-III	3	25	M	1.98	M	0.05	M	-
Majid zoea I	3	48	I	1.75	I	0.27	I	0.72

* Includes all 1976 oblique plankton samples.

† Includes only mapped cruises (cruise codes are explained in Appendix III).

O = Offshore: highest abundances offshore, caught at very few inshore stations.

M = Mid-Gulf: highest abundances at mid-Gulf stations, lower abundance both inshore and offshore.

I = Inshore: highest abundances inshore, generally not found beyond mid-Gulf stations.

† Maximum abundance was judged to reflect relative abundance between cruises as well as or better than other measures. It indicates the abundance in areas which often contain most of the total numbers found. Wide variations in abundance throughout the Gulf made average abundance less useful.

‡ Parentheses indicate two or fewer occurrences.

§ Both were identified as *Neocalanus cristatus*.

¶ Not identified.

Most of the forms in Group 1 were only found inshore to mid-Gulf, although some, such as *Tortanus discaudatus* (Figure 54) and pinnotherid zoeae IV–V, were dispersed in low numbers beyond mid-Gulf. The forms in Group 1 were, as a whole, dispersed farther offshore in the southern part of the Gulf than in the northern part and appeared to be within the lower salinity, higher temperature plume of San Francisco Bay water. Densities of most of these forms were highest at the most nearshore stations, particularly south of the Golden Gate area, to a lesser extent in Drake's Bay. *T. discaudatus* was highest in abundance in Drake's Bay in March and, along with pinnotherid zoeae IV–V, was also high in abundance in mid-Gulf areas on later cruises. During the May–June cruise Group 1 forms were absent or in very low numbers in Drake's Bay.

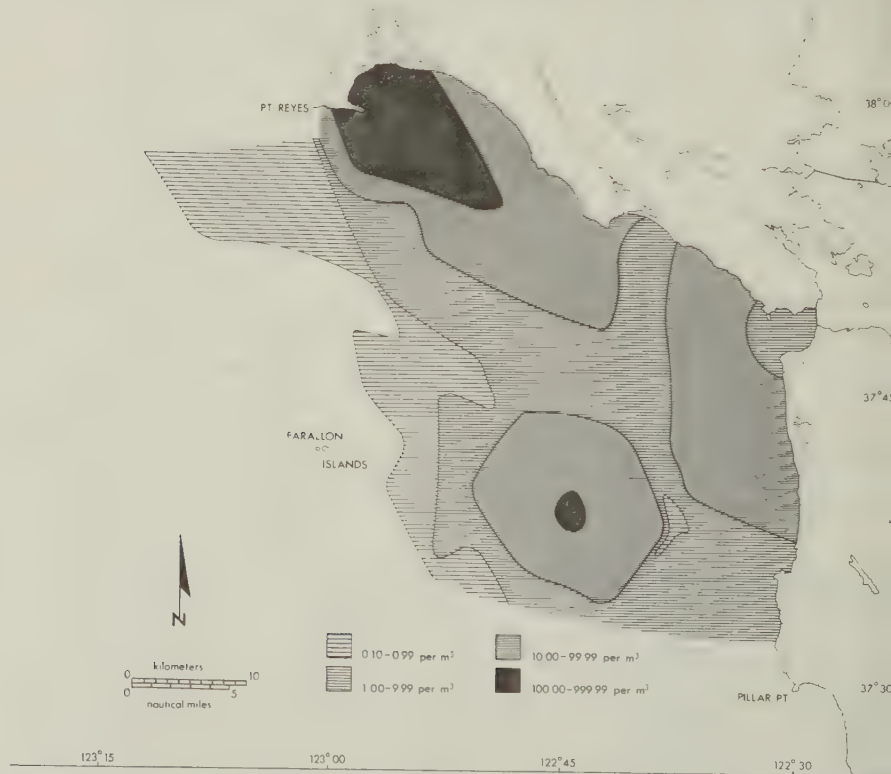


FIGURE 54. Distribution of *Tortanus discaudatus*, cruise 76301, March 18 to March 31, 1976.

Group 2 includes species which were more abundant offshore and those which were more abundant mid-Gulf. The mid-Gulf copepods *Calanus pacificus*, *Metridia lucens*, and *Acartia longiremis* were listed with the offshore species (rather than inshore species as in 1977) because of the more contracted distribution of the nearshore forms which was the result of sampling only during the upwelling season in 1976. Cross-group affinities between the first two groups are due to *C. pacificus*' affinities with all of Group 1, except the most inshore forms (*Cancer antennarius/gracilis* zoea I, grapsid zoeae I–III, and porcellanid larvae) and *M. lucens*' affinities with the forms spread farther into the Gulf (*T. discaudatus* and pinnotherid zoeae IV–V).

Groups 1 and 2 are quite separate as measured by the number of cross-group affinities. With very few exceptions the species in Group 2 were not found nearshore south of the Golden Gate on any of the cruises. The stations nearest Double Point and just below Drake's Bay provided the most common areas where offshore species occurred close to shore. This is similar to 1977, although the station below Drake's Bay did not yield as many offshore species in abundance as the 1976 cruises. The areas of highest abundance of offshore species varied by cruise. In March, the area of highest abundance was near the Farallon Islands, in April it was south offshore, and in May, north offshore.

Group 3 includes species not close enough inshore to have affinities with the most inshore species of Group 1, but also not distributed out far enough to belong in Group 2. It is, however, most closely allied with Group 1 (Figure 53).

Gulf to Cape Mendocino

The March 16–31, 1979 cruise extended from the Gulf of the Farallones to Cape Mendocino and farther offshore than cruises in 1976 and 1977. A number of overall distributional patterns emerged from this cruise.

A few holoplankton and many meroplankton species were found only close inshore (Table 16). Most, however, were captured out to stations farther from shore in the San Francisco area (Table 16, transects 5, 6, and 7) but only sporadically and in low numbers ($1.0\text{--}7.0/100^3$) at the most inshore stations (within 8–10 km) farther north. Exceptions were pinnotherid zoeae and the ctenophore *Pleurobrachia bachei*, the latter being comparatively higher in abundance ($46/100^3$) north and inshore, but with a similar overall distributional pattern. The euphausiid *Thysanoessa spinifera* was the only species caught in higher numbers at inshore stations over the whole area, north to south.

Table 16. Zooplankton Caught Predominately at Nearshore Stations on the March 1979 Cruise by Transect* and Farthest Offshore Station† Captured.

Species	Transects				
	1 & 2	3 & 4	5	6	7
<i>Callinassa</i> spp. larvae	1	0	0	3	6
<i>Cancer antennarius</i> zoeae II–III	0	0	0	3	6
<i>Cancer antennarius</i> zoeae IV–V	0	1	2	5	6
<i>Cancer antennarius</i> megalopa	0	1	4	3	6
<i>Cancer antennarius/gracilis</i> zoea I ‡	0	0	0	1	3
<i>Cancer gracilis</i> zoeae II–III	0	1	0	3	7
<i>Epilabidocera longipedata</i>	0	1	2	0	1
Grapsid zoeae IV–V	0	0	0	1	1
Pagurid larvae	0	1	3	3	4
Pinnotherid zoeae I–III	2	1	1	5	6
Pinnotherid zoeae IV–V	5	0	2	5	6
Pinnotherid megalopa	0	1	3	4	6
<i>Pleurobrachia bachei</i>	1	5	3	4	5
Porcellanid larvae	0	1	2	1	1
<i>Tortanus discaudatus</i>	0	0	0	1	3
<i>Upogebia pugettensis</i> larvae	0	0	0	1	0

* Transects 1 and 2, off Cape Mendocino; 3 and 4, off Pt. Arena; 5, off Pt. Reyes; 6 and 7, Gulf of the Farallones to offshore (Figure 16).

† Stations were numbered consecutively from onshore to offshore; a zero indicates that the zooplankton was not found at any stations on the transect.

‡ May be too small to be consistently caught in the 1.0-mm mesh net.

Another characteristic group of species was distributed predominantly beyond 30 to 50 km in the Gulf of the Farallones transects and a majority of these were absent within approximately 25 km of Cape Mendocino. Included among members of this group were copepods *Candacia bipinnata*, *Euchaeta japonica*, and *Euchaeta acuta*; euphausiids *Nematoscelis difficilis* and *Thysanoessa gregaria*; crabs *C. productus* zoeae IV-V and *C. oregonensis* zoeae IV-V; and a chaetognath *Sagitta scrippsae*.

No other onshore-offshore gradients or marked changes in abundance were obvious, although some offshore species were more abundant at night. The majority of these were copepods (Table 17). Two species, the crab *Chionecetes tanneri* zoea I and the chaetognath *Sagitta euneritica*, were caught more often during daylight.

TABLE 17. Results of Mann-Whitney U-tests for Differences in Median No./m³ of Individual Species for Day Versus Night Oblique Tows during March 1979 Cruise.

Species	Significance level	
	$P \leq 0.001$	$0.001 < P \leq 0.01$
<i>Caught predominantly at night</i>		
Copepods		
<i>Euchaeta japonica</i>	X	
<i>Euchirella galeata</i>		X
<i>Euchirella pulchra</i>	X	
<i>Gaidius pungen</i>	X	
<i>Lophothrix frontalis</i>	X	
<i>Pleuromamma abdominalis</i>	X	
<i>Pleuromamma quadrangulata</i>		X
<i>Pleuromamma xiphias</i>	X	
<i>Scottocalanus persecans</i>	X	
<i>Undeuchaeta bispinosa</i>	X	
Euphausiids		
<i>Euphausia pacifica</i>	X	
<i>Nematoscelis difficilis</i>	X	
Others		
<i>Cancer productus</i> zoeae I-III		X
<i>Clione limacina</i>		X
<i>Nanomia bijuga</i>		X
<i>Vibilia armata</i>	X	
<i>Caught predominantly during daylight</i>		
<i>Chionecetes tanneri</i> zoea I		X
<i>Sagitta euneritica</i>		X

In addition to onshore-offshore distributional patterns, north-south gradients in abundance were observed for some species found out to the most offshore stations. Nearshore species (Table 16) were not included in these determinations. The abundance of 16 species was significantly higher at Cape Mendocino transects than Gulf of the Farallones transects (Table 18). Eight species or larval forms were more abundant in Gulf transects than Cape Mendocino transects (Table 18).

TABLE 18. Results of Mann-Whitney U-tests for Differences in Median No./m³ of Individual Species from Oblique Tows on Transects 1 and 2 (Cape Mendocino) Versus 6 and 7 (Gulf of the Farallones) on March 1979 Cruise (Figure 16).

Species	Significance level		
	$P \leq 0.001$	$0.001 < P \leq 0.01$	$0.01 < P \leq 0.05$
<i>Caught predominantly at northern stations</i>			
Copepods			
<i>Neocalanus cristatus</i>	X		
<i>Neocalanus plumchrus</i>	X		
<i>Euchaeta acuta</i>			X
<i>Euchirella rostrata</i>	X		
<i>Heterorhabdus papilliger</i>		X	
<i>Heterorhabdus tanneri</i>			X
Mollusks			
<i>Clio pyramidata</i>			X
<i>Clione limacina</i>			X
<i>Corolla spectabilis</i>		X	
<i>Limacina helicina</i>	X		
Chaetognaths			
<i>Eukrohnia hamata</i>	X		
<i>Sagitta decipiens</i>			X
<i>Sagitta scrippsae</i>	X		
Others			
<i>Muggiae atlantica</i>	X		
Sergestid larvae.....			X
<i>Tomopteris septentrionalis</i>			X
<i>Caught predominantly at southern stations</i>			
Copepods			
<i>Calanus pacificus</i>		X	
<i>Lophothrix frontalis</i>		X	
Chaetognaths			
<i>Sagitta enflata</i>	X		
Others			
<i>Cancer gracilis megalopa</i>			X
<i>Cancer productus megalopa</i>			X
<i>Cancer productus zoeae</i> IV-V.....		X	
<i>Emerita analoga zoea</i> IV.....			X
<i>Liriope tetraphylla</i>		X	

Other species were either equally or similarly abundant throughout the area sampled (e.g. the copepods *Rhincalanus nasutus* and *Eucalanus bungii* and the chaetognath *Sagitta decipiens*) or were not abundant enough for me to draw any conclusions concerning their distributions.

DISCUSSION

The zooplankton populations sampled reflect seasonal changes in large scale current systems off California as well as more local phenomena such as upwelling events, relaxation of upwelling, and influence of the San Francisco Bay plume. Individual life histories, as well as interactions among species of the plankton community, undoubtedly play important roles in patterns of distribution and abundance. The spring rise in abundance of neritic copepods, for example, probably depends on the availability of high densities of phytoplankton (which we did not study) as a food source.

We sampled zooplankton during two distinct ocean seasons, the winter Davidson Current season and the spring upwelling season. Generalized current patterns for these seasons are well known (Reilly, Chapter 5; Wild et al., Chapter 14), although there are still uncertainties about localized smaller scale dynamics, driving forces, and currents at depth. In central and northern California, continental shelf waters generally move northward in winter, bringing warmer more saline water north alongshore. Further offshore the lower salinity California Current flows southward. As northwesterly winds intensify in the spring, the mean nearshore surface current reverses toward the south, and a characteristic mean vertical shear in velocity is established (Huyer et al. 1979). The California Current moves closer in toward the coast during this period. Nearshore surface water is transported offshore by Coriolis force during episodes of strong northwesterly winds and is replaced by upwelled, deeper, cooler water, rich in nutrients. Periodically during the upwelling season, winds slacken and warm offshore surface water moves inshore.

During our January 1977 cruise, surface temperatures were high (13.1–13.3 C) near and to the south and west of the Farallon Islands, and lower north and inshore (10.9 C at the Golden Gate). The combination of high temperature and salinity at the offshore stations indicates intrusion of warmer water from the south (Davidson Current) or offshore, rather than the less saline California Current water. The water in the Gulf of the Farallones was relatively uniform horizontally and vertically during this cruise. Many of the predominantly inshore forms were found further out in the Gulf or throughout the entire Gulf. Predominantly offshore species were, for the most part, also found throughout the Gulf. The faunal assemblage at this time was characterized in part by the low abundance or absence of northern species (Group 2, 1977), and in part by specific larval types which were caught only during this time as well as the appearance of species with southern or offshore affinities (Group 3, 1977).

During the spring cruises of 1976 and 1977, temperatures and salinities indicated varying degrees of upwelling. During the April 1977 cruise, much of the Gulf was dominated by surface temperatures below 10 C. The area of strongest upwelling was observed just outside Pt. Reyes where the lowest surface temperature (8.4 C) was recorded. Only at the San Francisco Bay mouth did we record a temperature above 11 C. Surface salinities were highest near Point Reyes at 33.9 ppt, while the rest of the Gulf was between 33.1 and 33.8 ppt. The San Francisco Bay mouth was lowest at 32.3 ppt. During most of the spring cruises, 15-m temperatures were 8 to 9 C. There was, however, more stratification than during the April 1977 cruise, with surface temperatures 1 to 2 C higher indicating that warm offshore surface waters were close inshore and upwelling was not reaching the surface. The San Francisco Bay mouth was consistently the warmest and freshest of the Gulf stations during the spring cruises. Other warm and less saline areas were the southern Gulf and the stations farthest offshore to the north. Surface temperatures in Drake's Bay ranged from a low of 8.6 C to a high of 11.1 C.

In contrast to the Davidson period, the spring upwelling season showed a more distinct separation of zooplankton into two distributional groups. During the upwelling season many neritic species and larvae of nearshore benthic species were only found close to the coast, while offshore species were for the most part found only in the outer half of the Gulf. The recurrent grouping in 1976

when all sampling was done during the upwelling season, showed this pattern most clearly. The separation of Group 2 from Groups 1 and 4 in 1977 (Figure 42) also reflects this distributional pattern. The mid-Gulf to offshore faunal assemblage during upwelling was characterized by species with northern affinities (Group 2 in both 1976 and 1977).

Some of the species and life-stages caught in the Gulf of the Farallones during the upwelling season were those which are also found in near surface waters in the sub-arctic. Marlowe and Miller (1975) studied vertical stratification of zooplankton populations at "Ocean Station P" in the Gulf of Alaska (lat 50° N, long 145° W). Such forms as *Parathemisto pacifica*, *Limacina helicina*, *Tomopteris* sp., *Neocalanus cristatus*, and *N. plumchrus*, all subadults, and the chaetognath *Eukrohnia hamata* stage I were most abundant at the surface or 25 m. Surface temperatures are colder at "Ocean Station P" than in central California and some submergence of these forms might be expected in central California. However, these forms were found in the Gulf during the April cruise in 1977 during strong upwelling. In addition, *Sagitta scrippsae* young, which are found in the upper 100 m of the California Current (Alvarino 1962), were also found in the Gulf at this time.

Deep dwelling life-stages, such as adult forms of *N. cristatus*, *N. plumchrus*, and *S. scrippsae*, were not caught in our tows. In addition, species which we captured predominantly at night on our March 1979 cruise (Table 17) were found only rarely, if at all, in our spring Gulf samples. Most of these species apparently occur primarily below 100 m (our maximum oblique tow depth) during the day and move closer to the surface at night. These observations suggest that upwelled water entering the Gulf probably does not come from great depth. Off Oregon, Halpern (1976) found that during short-period upwelling 8–10°C water at the surface originated at 25- to 50-m depth.

Upwelling due to wind stress may result in divergent fronts parallel to the coast as described by Peterson et al. (1979). Upwelling is often strongest near points of land which reach westward and gyres are common at capes and points during the upwelling season (Pirie and Steller 1977). Such phenomena undoubtedly influence zooplankton distributions.

The distributions of species in the Gulf of the Farallones during the upwelling season may be due in part to divergent upwelling fronts causing the separation between inshore and offshore groups of species. Other phenomena affecting the species distributions appear to be the gyre system, which dominates the northern half of the Gulf during upwelling episodes, relaxation of upwelling, and changes in brackish-water flows from San Francisco Bay.

Drake's Bay in the lee of Pt. Reyes and an area near and to the south of the San Francisco Bay mouth are two locations where large concentrations in inshore zooplankton are entrapped (e.g. Figure 45). There is often an area of lower zooplankton concentration between them at Double Point where many offshore species reach farthest into the Gulf both in winter and spring (e.g. *Limacina helicina*, Figure 52).

Landsat satellite photographs (e.g. Figure 41) analyzed by Pirie and Steller (1977) show a gyre reaching around Pt. Reyes into Drake's Bay above Double Point. Larger numbers of the cold-water chaetognaths *Eukrohnia hamata* and *Sagitta scrippsae* were found in the northern half of the Gulf during the upwelling season of 1977. Presumably the Pt. Reyes gyre concentrated them in that area.

Peterson et al. (1979) describe relaxed upwelling off central Oregon as a time when northwesterly winds weaken, surface water moves shoreward (from 20 to 40 km), and the permanent pycnocline may fail to reach the surface. Similar conditions apparently occurred in the Gulf in May 1977 when surface temperatures were warm (to 12.2 C) and upwelling had relaxed and was no longer bringing substantial numbers of cold water species into the Gulf. *Dolioteuthis gegenbauri* and *Oikopleura vanhoffeni* (Group 10), two surface-dwelling offshore species, moved toward shore.

During the upwelling seasons of both 1976 and 1977, the southern half of the Gulf was dominated, at least to mid-Gulf, by nearshore larval forms and San Francisco Bay copepods such as *Acartia clausi* and *Epilabidocera longipedata*. These inshore forms reached farther west in March 1976 than in April 1977 when the highest concentrations were found at our closest inshore station 5 nautical miles (9.3 km) from shore. This difference between 1976 and 1977 may be related to brackish-water flow through the Golden Gate. River water flow through the Sacramento-San Joaquin Delta into San Francisco Bay is estimated at Chipp's Island at the confluence of the Sacramento and San Joaquin Rivers by the California Department of Water Resources. Allowing for a 5-day lag from Chipp's Island to the Gulf, average flow during the April 1977 cruise was 2,796 cfs/day and had been even lower the week before. During the March 1976 cruise, average flow was 4,387 cfs/day and had been up to 25,000 cfs 10 days earlier.

The March 1979 cruise was conducted during the transition period between Davidson and upwelling seasons. After an interval of strong southerly winds, northwesterly winds began to blow steadily in late March (Figure 24). The nearshore southward flowing surface current characteristic of the spring-summer season apparently began off San Francisco shortly after our cruise ended.

An intriguing distributional pattern evident from the March 1979 cruise was the north to south difference in abundance and offshore extent of inshore larval and neritic forms. During this cruise, nearshore forms generally were found farther from shore and in greater abundance in Gulf transects compared to Farallone and Cape Mendocino transects (Table 16). The Gulf transects showed similarities to the pattern of the January 1977 cruise, with nearshore forms occurring to the outer edge of the Gulf and beyond. Uniformity of the water mass throughout the Gulf, a characteristic of the January 1977 cruise, was also apparent in late March 1979, although temperatures and salinities were low, indicating a higher percentage of California Current water and (or) possibly San Francisco Bay water. Low surface salinities (< 32ppt) observed out to 42 km from shore suggest that brackish-water flow was important in carrying zooplankton to the outer edge of the Gulf of the Farallones. It is possible that a divergent upwelling front could have held neritic forms so closely inshore at Cape Mendocino that we did not encounter many even in our closest stations at 5 nautical miles (9.3 km) from shore. Lower surface temperatures (10.0–10.3 C) and higher salinity (32.5 ppt) at these stations suggest that upwelling was occurring there during the cruise.

There were also some interesting distributional differences between larval *Cancer* crabs on this cruise. Late zoeal stages of *C. productus*, *C. gracilis*, and *C. magister* were all absent close to shore near San Francisco, whereas *antennarius* late stages remained in close. *C. gracilis* megalopae and *C. productus*

oeae IV-V and megalopae predominated in the southern transects. One can speculate that combinations of differences in size, swimming ability, buoyancy, adult population distributions, and timing of release and development of these larvae account for their distributions.

Some year-to-year variation in extent of alongshore zooplankton movement is evident in comparing chaetognath distributions in our 1977 samples with CalCOFI samples. Alvarino (1965) analyzed CalCOFI samples from 1954 and 1958; 1954 was a cold-water year ($< 11^{\circ}\text{C}$ in the Gulf of the Farallones in June), and 1958 a warm-water year ($> 13^{\circ}\text{C}$ in the Gulf in April; $> 12^{\circ}\text{C}$ in July). Overall, temperatures were lower along the coast during both Davidson and upwelling seasons in 1954 than 1958. In 1958, the chaetognath *S. enflata*, a warm water species, was found in relatively high numbers ($> 50/100\text{m}^3$) north to about San Francisco in January, and continued to be found in low numbers off San Francisco in April, May, and June. In January 1954, *S. enflata* was lower in numbers off Pt. Conception (approximately lat $34^{\circ} 5' \text{N}$) compared to 1958 (no samples were taken any farther north in January 1954). In late April and June 1954, no *S. enflata* were found above Pt. Conception.

Complementary to the occurrence of *S. enflata* are the distributional occurrences of two, more northern, cold water chaetognaths. *S. scrippsae* is found in the upper layers of the California Current (Alvarino 1962 and 1965) and *E. hamata* is a cosmopolitan species reported to be primarily below 100 m south of the arctic (Bieri 1959; Alvarino 1965), although we found it in the Gulf during the upwelling season.

In 1954, *S. scrippsae* was caught as far south as northern Baja California early in the year (January through March) and reached south of Pt. Eugenia (about mid-Baja California) by the April-May cruise. It was moderately abundant ($0.5\text{--}1/100\text{m}^3$) off San Francisco during April-May (the first cruise as far north as San Francisco that year) and June. In 1958, the southern distribution of *S. scrippsae* extended only to the vicinity of the California-Baja California border during both winter and spring and was much less abundant off San Francisco compared to 1954.

In 1954, *E. hamata* was first found in CalCOFI samples in March near Pt. Conception and, thereafter, occurred sporadically south of Pt. Conception. Off San Francisco it was most abundant in June when it was caught throughout the area from Monterey Bay to nearly Cape Mendocino, the northernmost transect occupied that year. In 1958, *E. hamata* was found sporadically off central and southern California in April and May but, in June, was found only as far south as San Francisco, and only at one station, off San Francisco.

Conditions in the Gulf in 1977 were apparently between the extremes observed in 1954 and 1958. In January 1977, *S. enflata* was found in the Gulf in substantial numbers indicating northward-flowing water nearshore. No other predominantly southern species were found. The 1977 upwelling season was marked, at least in April, by both low temperatures and northern species entering the Gulf. Certainly the year was not similar to the "warm-water year" 1958, but how much it was like the "cold-water year" 1954 is difficult to say. Because sampling in 1976 did not include January or February, that year cannot be characterized similarly.

I analyzed a limited number of samples from a January 1978 cruise. That year, we frequently caught the southern copepod *Pontellopsis occidentalis* in low

numbers, and comparatively larger numbers and a larger diversity of offshore hyperiid amphipods. These data indicate the winter of 1977–78 may have had stronger northward flowing currents than winter 1976–77.

An important question for zooplankton dispersal from the Gulf is not only the origin of the water but its destination, and thus where larvae hatched in the Gulf of the Farallones-Bodega Bay area will be transported. One predominantly southern species which may be a reliable indicator of northward moving nearshore water is the chaetognath *S. enflata*. Renshaw (1962), sampling monthly for chaetognaths approximately 20 to 50 km (12.5 to 31.2 miles) west of Dillon Beach (about 50 km north of San Francisco), captured *S. enflata* only in December. Two of 12 drift bottles Renshaw released in December were recovered, one near the California-Oregon border, and the other in Oregon. This is in conformity with the northward set of a series of surface drifters released during December–February 1970–71, seaward of 25 km from the Golden Gate (Conomos et al. 1971), and analysis of satellite photographs taken from 1973 to 1977 (Pirie and Steller 1977). Thus, Gulf zooplankton would most likely be carried northward in winter.

Seasonal shifts in chaetognath distributions evident in 1954 and 1958 (Alvarino 1965) demonstrate southward alongshore water movement in the spring. While Alvarino's data are sparse above Pt. Conception, a change in abundance and distribution is discernible (as discussed earlier) at the northern reaches of the range of *S. enflata* near San Francisco in the spring. In both 1954 and 1958, Alvarino found *E. hamata* off central and southern California only in March or later. For *S. scrippsae*, the northernmost stations of each cruise characteristically had higher abundances than those at the southern edge of its distribution especially during spring, indicating the major portion of the population was to the north. Extension to the south was particularly noticeable in spring 1954 (the colder water year) when its distribution extended below Pt. Eugenia from April through June.

My observations in central and northern California agree with the seasonal timing of these alongshore extensions of chaetognath distributions. March to early April appears to be the critical time when the California Current begins to bring northern species south and nearshore. *S. enflata* was present in the Gulf during January 1977, but was later replaced by more northern species including *S. scrippsae* and *E. hamata*. Our March 1979 cruise gives evidence of having occurred near the transition time. *S. enflata* was low in numbers both in the Gulf and offshore, while both *S. scrippsae* and *E. hamata* were not evident in the Gulf, were low in numbers farther offshore from San Francisco ($\bar{x}$'s = 0.2 and 0.03/100m³, respectively), and were markedly higher in numbers to the north at Cape Mendocino ($\bar{x}$'s = 1.1 and 2.7/100m³) where they were found both nearshore and offshore. This was also the pattern of such northern affinity species as *Neocalanus cristatus* and *N. plumchrus*.

The spring transition in current direction for the central Oregon Coast in 1975 occurred between mid-March and mid-April (Huyer et al. 1979). The timing of this transition in central California may have been similar in 1979. Just after the spring transition, coastal surface water (0- to 25-m depth) off Oregon moves southward at a mean rate of 40–45 cm/sec (24.3 miles/day) (Halpern 1976; Huyer et al. 1979). Zooplankton off Cape Mendocino carried southward at this rate would take approximately 8 days to reach the Gulf of the Farallones. Thus,

surface dwelling species could be moved southward quickly.

Dungeness crab larvae presumably would be carried northward by along-shore currents from January to mid-March and southward as megalopae in April. They would move farther north in a warm-water year and farther south in a cold-water year. It is possible that more recruitment of Dungeness crab larvae from the larger populations to the north may occur in central California during a cold-water year, while very little may occur during a warm-water year when currents would be expected to move the larvae farther north. However, factors affecting recruitment to the adult population appear to be much more complex and may also include spawning stock size; egg, larval, and juvenile survival; predation; pollution; etc.

It is striking that the time of transition in the currents is also the time at which molting of Dungeness crab larvae from stage V zoeae to megalopae is taking place. Late stage megalopae appear in concentrations inshore after the transition period. Timing of the transition may be critical in the movement of megalopae back inshore, although the mechanism for this movement is unclear. Also, it appears that nearshore zooplankton were distributed farther outward from the Gulf of the Farallones than along the northern coast, at least during the transition period. The distribution of these zooplankton probably reflects processes occurring during the late Davidson period as well. Parrish et al. (1981) state that during winter Ekman transport is directed toward the coast in the Pacific Northwest region while south of Cape Mendocino transport is offshore, increasing in strength to the south. This is consistent with zooplankton distributions I observed and presumably could cause a higher loss of Dungeness crab larvae offshore in the southern area. Thus, recruitment from the north could be important to offset such losses.

In summary, there is evidence from zooplankton distributions of inshore-offshore and alongshore movement of surface dwelling zooplankton found in the Gulf. The general direction of alongshore movement, dependent on season, is northward in winter and southward in spring. Dungeness crab zoeae appear to move offshore and presumably alongshore during late winter and the winter-spring transition period. After upwelling begins, the megalopae appear in concentrations nearshore, although the mechanism by which they move inshore is unclear.

A complex system of currents within the Gulf of the Farallones is evident. While affected by the larger seasonal alongshore systems, species populations also reflect upwelling processes related to wind stress and topography (e.g. the presence of Pt. Reyes to the north) and outflow from San Francisco Bay. Areas of high zooplankton densities are presumably entrainment areas where zooplankton species accumulate and (or) reproduce without being substantially dispersed. Such areas in the Gulf of the Farallones are Drake's Bay, the vicinity of the San Francisco Bay mouth, and the nearshore area south of the Bay mouth. The first two appear to be important crab megalopal settling areas, while the third is an area where many San Francisco Bay zooplankton species are found in great abundance.

Chapter 9

MOVEMENT AND GROWTH OF POST-LARVAL DUNGENESS CRABS, *CANCER MAGISTER*, IN THE SAN FRANCISCO AREA

by

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Menlo Park, California

INTRODUCTION

Responding to the long-term low landings in the San Francisco fishery, the Department's Shellfish Investigations initiated a study in 1971 to determine elements of movement and growth in Dungeness crabs. This study was carried over as part of the Dungeness Crab Research Program when it began in 1974.

Over the years, Dungeness crabs have been tagged for movement and growth studies using a variety of methods. Paint, mutilation, internal tags, and external Peterson disc tags were tried by Waldron (1958) in Oregon. Waldron was most successful with the Peterson disc tag, although it was shed when the crab molted. Attempting to eliminate loss due to molting, Butler (1957) used a stainless steel wire suture tag developed for the Atlantic blue crab, *Callinectes sapidus*, on Dungeness crabs in the Queen Charlotte Islands region of British Columbia. In 1961, Snow and Wagner (1965) conducted a tagging study in Yaquina Bay, Oregon employing Butler's methods, with the exception that vinyl-plastic spaghetti and dart tags were substituted for the surgical wire.

Age and growth studies have been conducted throughout much of the range of the Dungeness crab by a variety of investigators. The first of these studies was made in British Columbia by MacKay and Weymouth (1935), followed by Cleaver (1949) in Washington, Butler (1961) in British Columbia, and Poole (1966) in Bodega Bay, California.

My study analyzes movement and growth of post-larval Dungeness crabs in the San Francisco area.

MATERIALS AND METHODS

Gear used to capture Dungeness crabs included ringnets with 1-inch (2.5-cm) mesh, a 16-ft (4.8-m) otter trawl with 1.5-inch (3.8-cm) stretch mesh and a 0.5-inch (1.3-cm) stretch-mesh liner in the cod end, and 40-inch (1.0-m) commercial type crab traps with no escape ports.

Monthly collections of crabs were made in the San Francisco-San Pablo Bay complex from 1971 to 1975 with ringnets and otter trawls. Crab traps were fished in the Gulf of the Farallones during preseason surveys. Sex was determined for crabs collected and carapace width (CW) was measured to the nearest millimeter just anterior to the 10th anterolateral spines.

¹Present address: California Department of Fish and Game, Eureka, California.

Crabs were tagged with blue Floy FT-4 spaghetti tags using $1\frac{1}{8}$ -inch (2.9-cm) stainless steel, $\frac{1}{2}$ -circle surgical needles, and international orange Floy FL-67 anchor tags using the FD-67 tagging gun and a holding box described by Snow and Wagner (1965). Both spaghetti and anchor tags were numbered and engraved "Return Calif. Fish and Game". Spaghetti tags were inserted through the carapace into the branchial chamber along the epimeral line anterior to the insertion of the last leg. Tags were threaded through two holes spaced $\frac{9}{16}$ inch (1.4 cm) apart and the loose ends secured with an overhand knot approximately 2.5 cm out from the carapace to allow room for growth. Anchor tags were inserted through the carapace at the same location as the spaghetti tags and were anchored by virtue of their T-shaped nylon head (Figure 55). A cash reward of \$1.00 was paid in 1971 and \$2.00 thereafter for returned tagged crabs. Tagging and return locations were recorded.

Instar sizes of male crabs were calculated from molts of crabs collected in the study area. Molts of both Bay- and ocean-reared crabs were used. The majority of juvenile crab molts were from San Francisco Bay, whereas most molts of adult crabs came from the ocean. Females were not used due to limited availability of molting records. Crab molting data came from several sources: (i) return of tagged crabs which had molted once prior to recapture, (ii) field observations of crabs which could be matched with cast shells, and (iii) crabs which were captured near molting and held in the laboratory until ecdysis occurred.

Crabs were aged by superimposing calculated post-larval instar sizes on carapace width frequency distributions.

RESULTS

During 1971, 1,105 crabs were tagged in San Francisco Bay. In 1972, 4,993 crabs were tagged, 3,080 in the San Francisco-San Pablo Bay complex and 1,913 in the Gulf of the Farallones and Bodega Bay (Figure 56). During the 4 years of the tagging study no crabs tagged in the Gulf of the Farallones were recaptured in San Francisco Bay or San Pablo Bay. Sixty-four juvenile crabs tagged in the Bay were caught within 90 days of tagging at the tagging site. Fifty Bay-tagged crabs were recaptured in the Gulf of the Farallones. One male crab tagged near Richmond remained at liberty for 3.5 years before recapture north of Pt. Reyes near Abbotts Lagoon. The record for movement went to a crab which traveled at least 53 miles from Crockett to Pt. Reyes. Seventy-three recaptured crabs molted while at liberty; of these, 52 molted once, 16 twice, and 5 three times. Only four adult females (of 483 tagged) were recaptured, one of which had molted.

Mean, range, and standard deviation of carapace widths of male Dungeness crabs from the north San Francisco Bay-San Pablo Bay complex were summarized and plotted by month from January 1974 to December 1975 (Figure 57). After September few crabs other than crabs-of-the-year were found in the Bay.

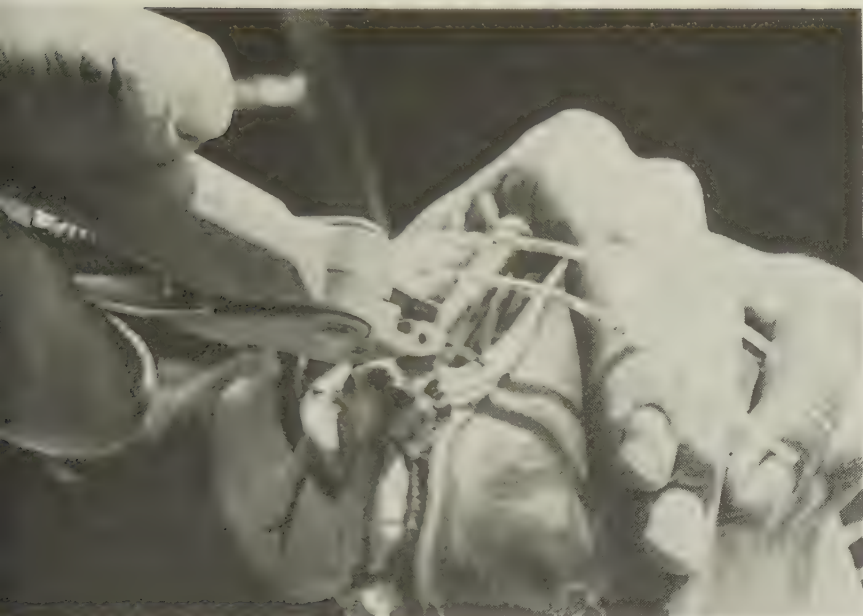


FIGURE 55. TAGGING OF DUNGENESS CRABS.



FIGURE 56. Location and number of Dungeness crabs tagged and recaptured from 1971 to 1975.

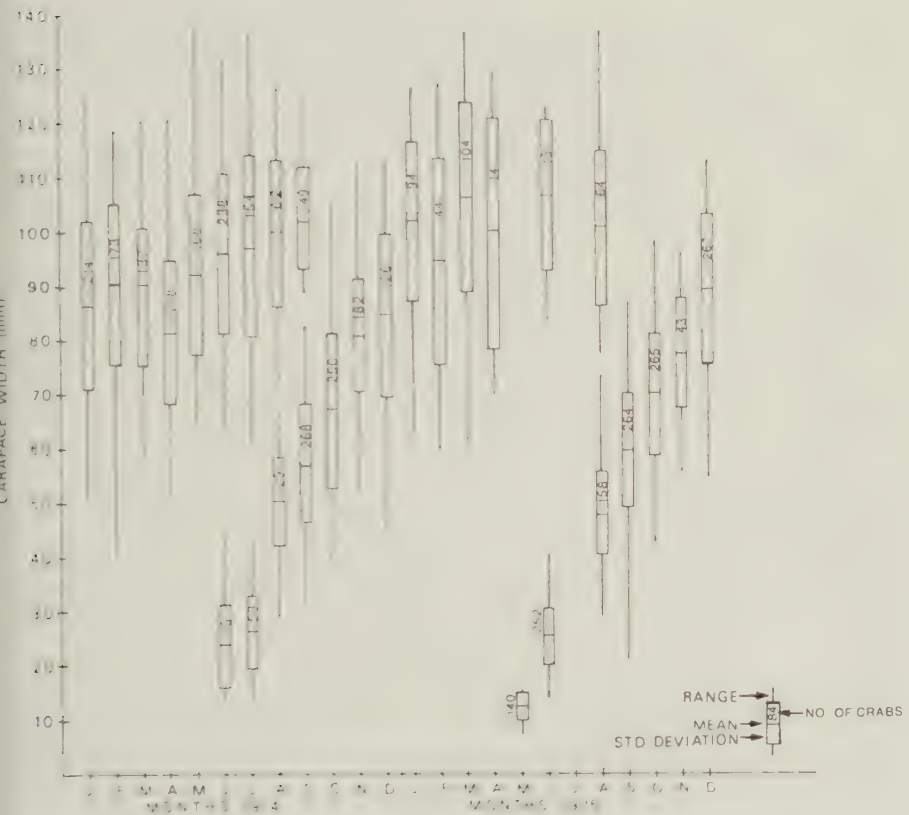


FIGURE 57. Growth data for male Dungeness crabs (N = 4,056) from the north San Francisco Bay-San Pablo Bay complex.

Graphic analysis indicated that a change in growth rate occurs at about 100 mm in male crabs (Figure 58). On this basis we divided male crabs into two groups, those with beginning carapace widths less than 100 mm and those with beginning carapace widths equal to or greater than 100 mm, and fitted two lines by least squares regressions using carapace width before molting as the independent variable, and carapace width after molting as the dependent variable.

For male crabs with beginning carapace widths less than 100 mm,

$$X_{i+1} = 1.0529 + 1.2233X_i;$$

while for male crabs equal to or greater than 100 mm,

$$X_{i+1} = 19.532 + 1.0515X_i;$$

where: X_i is the width in mm of the i^{th} instar.

The fourth post-larval instar at a carapace width of 18.4 mm was used as a starting point to calculate the other instar sizes (Table 19) because more information was available for this instar than for other instars. The first post-larval instar carapace width of 7.3 mm came from field observations rather than the calculated width of 7.9 mm, and thus was more accurate.

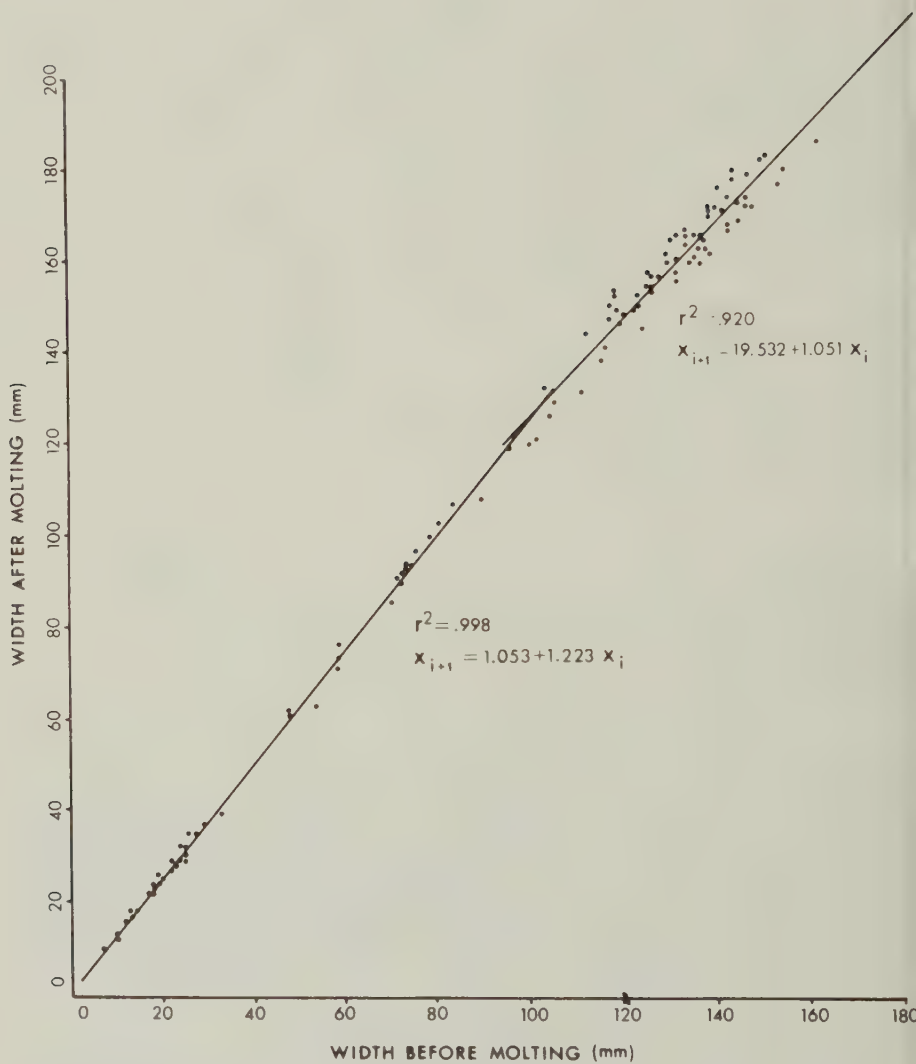


FIGURE 58. Growth rate of Dungeness crabs.

TABLE 19. Comparison of Computed Widths of Male Dungeness Crab.

Instar number	Crab carapace width (mm)*		
	Central California	Washington	Queen Charlotte Island
1	7.3	5 to 7	6.5
2	10.7	8.8	9.4
3	14.2	11.7	12.9
4	18.4	15.7	17.3
5	23.6	22.0	22.6
6	29.9	28.4	29.1
7	37.6	34.7	37.0
8	47.0	44.1	46.6
9	58.6	55.8	58.4
10	72.7	68.0	72.7
11	90.0	84.6	90.2
12	111.2	105.9	111.5
13	136.5	129.2	137.1
14	163.0	154.9	164.5
15	190.9		193.7
16	220.3		224.9

* Data for Washington and Queen Charlotte Island, British Columbia from Butler (1961)

DISCUSSION

Examination of carapace width-frequency distributions of crabs captured in San Francisco and San Pablo Bays during 1974 and 1975 (Figure 57) reveals that crabs of the year enter the Bay complex during May and June and leave by August or September the following year. The same pattern was also present during the period from 1970 to 1973 (Orcutt et al. 1975b). Crab tag recovery data show a regular pattern of movement of juvenile crabs out of the Bay complex and a random movement of adult crabs in the ocean (Figure 59).

MacKay and Weymouth (1935), studying growth rates and molting increments in British Columbia, stated that on the basis of molting and width frequency measurements, male crabs reached 165 mm (6.5 inches) including spines after 7 or 8 years. In Washington, Cleaver (1949) found that the majority of male crabs reached the legal size of 159 mm (6.25 inches), excluding spines, in 4 years. Butler (1961), in related studies in British Columbia, found that male crabs around the Queen Charlotte Islands reached 170 mm (6.9 inches) during their 4th year, a faster growth rate than found by MacKay and Weymouth (1935), but similar to that found by Cleaver (1949). I converted Butler's (1961) carapace measurements to exclude spines for comparison with my growth study using the formula

$$X = \frac{y + 0.029}{1.0715},$$

where: X equals carapace width exclusive of 10th anterolateral spines, and y equals carapace width including spines.

The computed post-larval instar sizes for San Francisco and San Pablo Bays differ very little from the sizes reported by Butler (1961; Table 19) and Cleaver (1949).

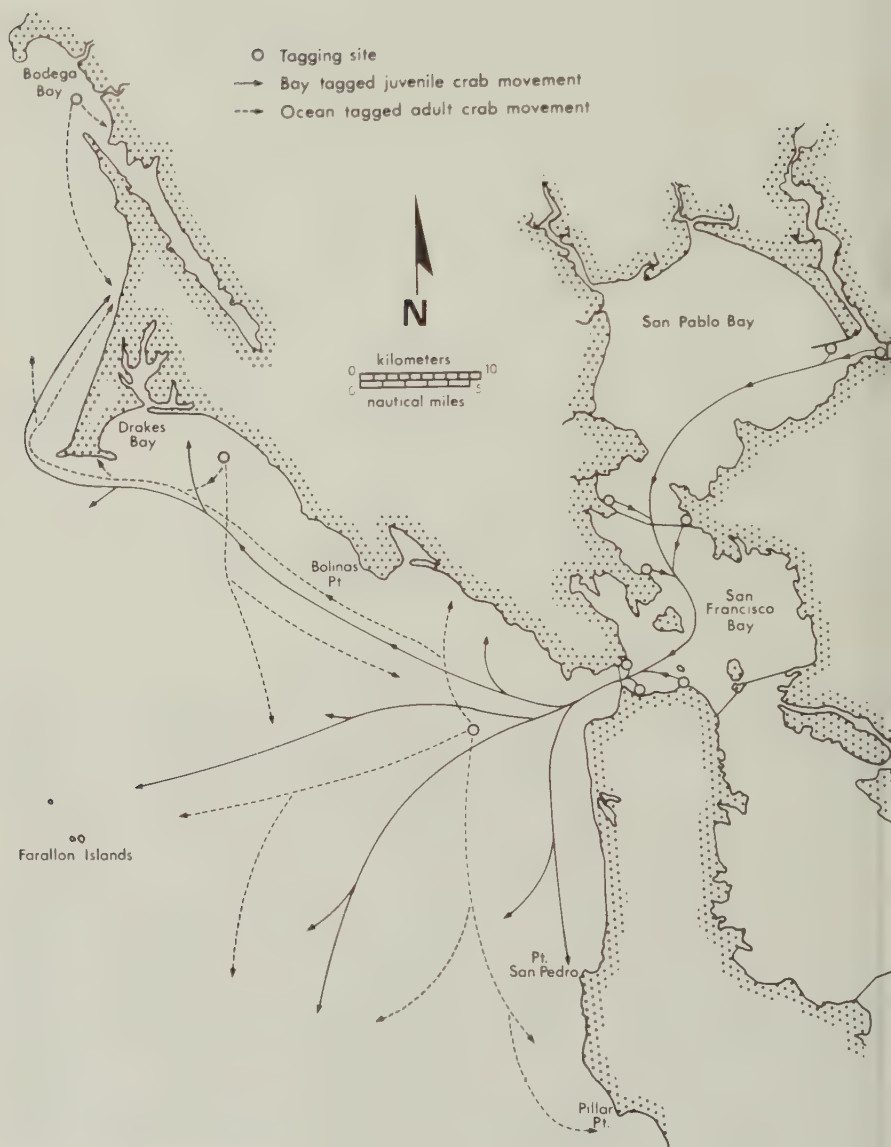


FIGURE 59. Movement of Dungeness crabs in the San Francisco area as indicated by tag recoveries.

While attempting to estimate age by superimposing calculated instar sizes on carapace width-frequency distributions, I encountered the problem that carapace width-frequencies begin to blend together after the first six or seven postlarval instars. The absence of well defined modes makes it difficult to estimate with accuracy the instar of a specific crab or the mean instar of a group of crabs. I believe, however, that gross assumptions about age at a given size can be made.

Because Dungeness crabs leave the north San Francisco Bay-San Pablo Bay complex at approximately 1.5 years of age, comparisons of growth rates were made when the crabs were 1 year old. In the Queen Charlotte Islands, British Columbia, Butler (1961) found that male crabs reached the sixth post-larval instar at 29.1 mm at the end of their 1st year, aged from time of hatching, and the 12th instar at 111.5 mm by age 2 years. This growth rate is similar to that found by Cleaver (1949) in Washington. Cleaver (1949) concluded that after 2 years a size of 95 mm was attained. Poole (1967) found that at age 1 year, male crabs from Bodega Bay had a mean size of 45 mm, and 130 mm at the end of 2 years. Over a 5-year period the average size range at 1 year in the San Francisco Bay-San Pablo Bay complex was 87 to 105 mm with four of the years averaging over 102 mm. The single mode in carapace width frequency histograms and the crabs' annual movement into and out of the San Francisco Bay-San Pablo Bay complex suggest that we are dealing primarily with a single year class in the Bay where more frequent molting results in a faster growth rate compared to other areas.

There was little apparent difference in the magnitude of growth increments between the different sources of molting data from the field, thus they were considered together. Although numerous molts of laboratory-held crabs were observed and recorded, they were not considered here because the increase per molt was noted to be consistently less than that observed in the wild. Stunting is a common problem in laboratory rearing of Dungeness crabs (Earl Ebert, Calif. Dep. Fish and Game, pers. commun.).

When carapace widths before molting are plotted against carapace widths after molting, an abrupt slowing of the growth rate is observed (Figure 58). This change in growth rate corresponds with onset of sexual maturity. The intersection of the two lines at 107.5 mm agrees well with the fact that in California all examined male Dungeness crabs greater than 122 mm were sexually mature, while none less than 93 mm were found to have mature spermatophores (Poole 1967). Butler (1961) working in the Queen Charlotte Islands found the change in growth rate at 108.2 mm which agreed with sizes at maturity determined earlier (Butler 1960). Cleaver's (1949) data showed that crab growth in Washington changed at 100.2 mm. Thus, the change in growth rate at or near sexual maturity is fairly consistent from British Columbia to California.

In summary, this study shows that size increments per molt for post-larval instars are similar from British Columbia to central California, but that crabs molt more frequently and growth rates are faster in central California. Crabs in the San Francisco Bay complex molt more frequently and grow at a rate about twice as fast as ocean-reared crabs. The Bay population consists primarily of one year class which enters the Bay about May-June and leaves by September of the following year. A slowing in growth rate of male crabs occurs at about onset of sexual maturity; growth rate change for females was not analyzed.

Chapter 10

JUVENILE DUNGENESS CRAB, *CANCER MAGISTER*, STUDIES IN THE SAN FRANCISCO BAY AREA

by

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INTRODUCTION

To even the most casual observer, the urbanization of San Francisco Bay, and the myriad of problems associated with it, have been apparent for decades. Only recently, however, have San Francisco and San Pablo Bays (Figure 12) been recognized as nursery areas for large numbers of juvenile Dungeness crabs (Walter Dahlstrom, Calif. Dep. Fish and Game, pers. commun.) which presumably are recruited into the San Francisco area fishery in the Gulf of the Farallones (Figure 11). The juxtaposition of these two situations made it imperative that the Dungeness Crab Research Program investigate details of the relationship between the Bay nursery and the Gulf fishery. This paper describes life history conditions for Bay-reared crabs, makes comparisons to ocean-reared crabs, and assesses the extent to which the Bay contributes to the fishery. Research on distribution, abundance, growth, and food habits are presented and discussed.

METHODOLOGY

Juvenile crabs were collected principally by trawl and hand-operated ringnets, and occasionally from fish stomachs. Trawling was done with 8-ft (2.4-m) beam and 16-ft (4.8-m) or 43-ft (13-m) otter trawl nets, constructed with 1.25-inch (3.2-cm) stretch-mesh nylon netting and 0.5-inch (1.3-cm) stretch-mesh nylon liners. Ringnets (Figure 1) had a 30-inch (0.8-m) diameter outer ring, 23-inch (0.6-m) diameter inner ring, and 1.75-inch (4.5-cm) stretch-mesh nylon netting. Smaller mesh ringnets were used occasionally when early post-larval crabs were available.

Research cruises were conducted from 1975 to 1979 (Appendix III). Spring cruises using trawls investigated timing, distribution, and stage of newly settled post-larval instars. Trawling in September–October measured catch-per-unit-effort (CPUE) for Gulf- and Bay-caught year class crabs. Late fall through winter trawling and ringnetting from boats provided information on distribution and abundance in San Francisco and San Pablo Bays. A 3-year (1977 to 1980) monthly ringnet survey, conducted from 15 to 17 shore-based stations (Figure 60; Appendix VI), provided data on distribution, relative abundance, and growth of juvenile crabs throughout the entire San Francisco-San Pablo-Suisun Bay complex. Crabs analyzed for food habits were caught by trawl and ringnet.

Crabs collected in the field were sexed, measured to the nearest millimeter carapace width (CW), excluding 10th anterolateral spines, and returned to the water unless retained for other studies. Crabs retained for stomach content

analysis were placed in 10% buffered formalin and returned to the Menlo Park Laboratory. Salinity and temperature were measured routinely at sampling locations.

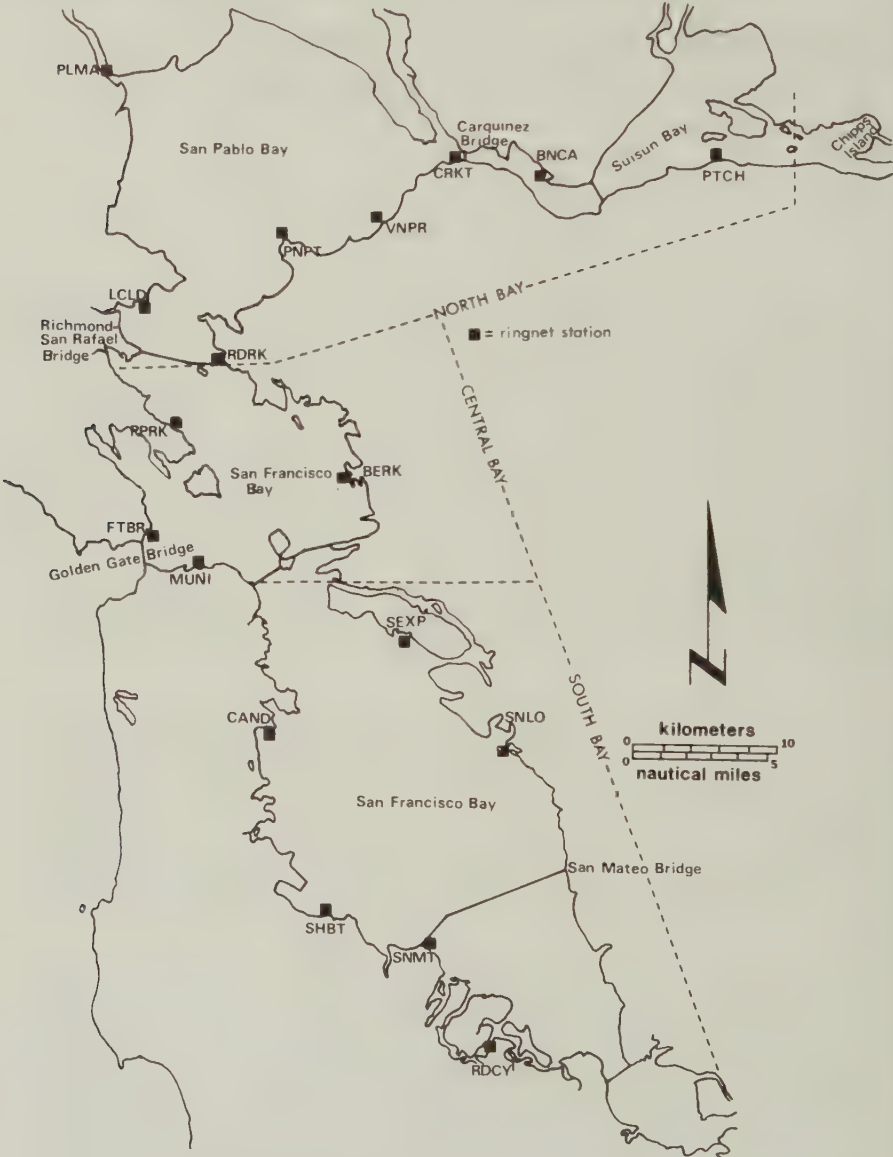


FIGURE 60. Station locations for shore-based ringnet survey (See Appendix VI).

RESULTS AND CONCLUSIONS
Distribution

Bay
From the many plankton samples and fish stomachs collected eastward of the Golden Gate (Reilly, Chapters 6 and 11), it is apparent that most Dungeness

crabs do not enter the Bay as megalopae, but as early post-larval instars. Early post-larval crabs, which have molted from the megalopal stage in the vicinity of the Golden Gate, presumably are swept by currents into the Bay along the bottom. Early instar crabs were first collected in the Bay each year from 1975 to 1979 on May 25, 27, 13, 28 and 5, respectively. Most early post-larval instars were captured near natural or maintained ship channels north of the San Francisco Bay entrance (Figure 61).



FIGURE 61. Bay collection sites for early post-larval instar crabs.

It takes approximately 4 months for Bay-reared crabs to reach the ninth post-larval instar at approximately 53 to 66 mm CW (Collier, Chapter 9). Crabs in this stage were found spread out over much of the Bay system and were most abundant in San Pablo Bay (Figure 62). The bulk of these crabs was collected during September–October sampling.



FIGURE 62. Bay collection sites for ninth post-larval stages.

Maximum dispersion of crabs-of-the-year was apparent from September through December. Crabs were found throughout much of the study area and there were concentrations along the shoreline near piers, jetties, marinas, boat launching ramps, and other sites offering protection. However, they were conspicuously absent from the shallow mud flats that dominate much of south San Francisco Bay, the eastern portion of central San Francisco Bay, and north and west San Pablo Bay (Figure 63). The distribution of juvenile crabs in the Bay covered approximately 500 km².



FIGURE 63. Bay collection sites for 0-age class crabs, September through December 1975–1979.

Routine trawling and ringnetting conducted during April–May showed a marked tendency by 1-year-old crabs in central and north Bay to consolidate near channel areas (Figure 64). Most of these crabs were in the 11th and 12th post-larval instar, 81.4 to 123.9 mm cw (Collier, Chapter 9). In the south Bay, only shore-based stations yielded crabs. May and June generally brought a mixing of outgoing and incoming year classes. By September, replacement of the old year class by the new was, for all practical purposes, complete.



FIGURE 64. Bay collection sites for 1-year-old crabs, April through May 1975–1979.

A small contingent of juvenile crabs is usually found each year inside the mouth of the Russian River north of Bodega Bay (Figure 17). On occasion, these crabs are prevented from being recruited into the San Francisco area fishery by formation of a sand bar at the river's mouth (Walter Dahlstrom, Calif. Dep. Fish and Game, Pers. Commun.). However, their importance to the fishery is minimal.

Ocean

Juvenile crabs were found distributed nearshore along sandy, shallow areas between Bodega Bay and Pt. San Pedro (Figure 65). The vast majority of these

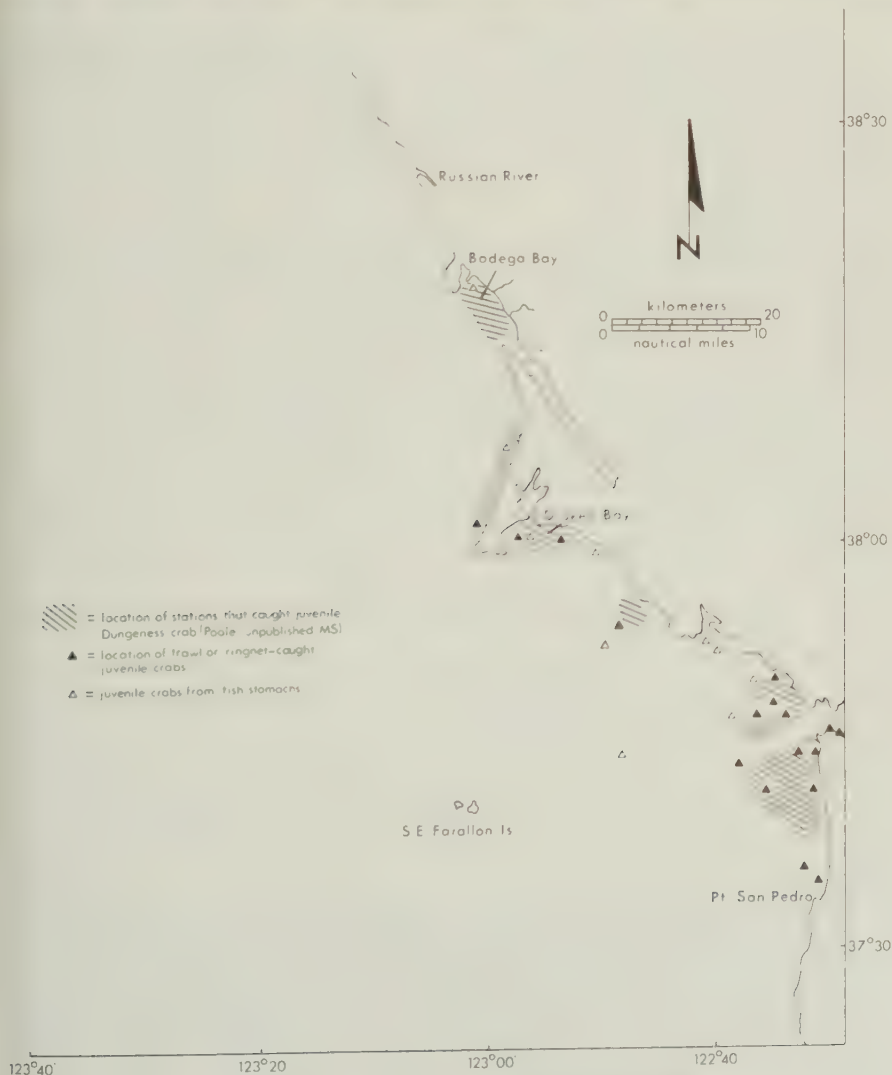


FIGURE 65. Distribution of juvenile Dungeness crabs in ocean areas.

crabs were found within 10 fm (18 m) and the rest within 20 fm (37 m). One exception was the occurrence of two second-stage post-larval instars in the stomach of a Pacific staghorn sculpin, *Leptocottus armatus*, caught 30 km out from the Golden Gate in 29 fm (53 m). Generally we found that the distribution of ocean-reared juvenile crabs remained relatively constant over the years of the study. I estimate the total area of juvenile crab distribution within the San Francisco fishery area to be approximately 500 km² (Figure 65), about equal in total area to Bay nursery habitat.

Abundance

Bay

The annual distribution of crabs in the Bay (Figures 61–64) was determined by combining trawl, ringnet, and fish stomach data; of these, our best source of information on relative abundance was the shore-based ringnet survey. During this monthly survey the consistency of effort (three 30-min sets with five ringnets during slack current) enabled us to document spatial and temporal differences in the population structure.

The greatest numbers of crabs were found throughout the year at north Bay stations, and station abundances remained fairly constant until onset of the rainy season. Following the initial heavy rains of the season, freshwater run-off from the Delta significantly reduced salinities throughout the Bay (Figure 23). Major reductions in crab abundance and shifts in location of crab concentrations occurred concurrently with reduced salinities (Table 20; Figure 66). No crabs were caught at any station where bottom salinity registered less than 10.2 ppt. Three of four stations recording increases in catch-per-ringnet from October to February were located near the ship channel. Substantial numbers of crabs were found well up the estuary at Benicia (BNCA) and Port Chicago (PTCH) (Figure 60) during the 1977 drought. Catch totals (Table 20) show the relative weakness of the 1978 year class, a condition also noted for both megalopae and juvenile crabs by Reilly (Chapters 6 and 11).

TABLE 20. Frequency of Occurrence of Juvenile Crabs in Shore-based Ringnet Survey, June 1977 to March 1980.

Year class	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Total
1977.....	10	143	543	578	707	676	801	341	144	69	74	55	4141
1978.....	—	1	21	77	176	149	59	91	82	95	81	—	832
1979.....	—	95	751	1049	505	233	208	142	19	52	—	—	3054
Total	10	239	1315	1704	1388	1058	1068	574	245	216	155	55	8027

Ocean

Inasmuch as the shore-based ringnet survey could only be conducted in the Bay, we relied on comparisons of trawl densities to determine relative abundance of 0-age class (<1-year old) Dungeness crabs in the Gulf (Figure 67). The Pt. Reyes area was the most productive overall, providing 55% of the total ocean catch with just 14% of all successful trawls. During the course of the study, however, only 41% of the trawls in the Pt. Reyes area were successful in capturing 0-age class Dungeness crabs. Additional data are available from Wickham et al. (1976), who collected 0-age class crabs in Bodega Bay on three



FIGURE 66. Catch-per-unit-effort for shore-based ringnet survey, 1975–1980.

separate occasions in 1973. Combining the results of Wickham et al.'s successful and unsuccessful trawls, I calculated that Bodega Bay densities ranged between 19 and 26 crabs per 1000 m². We were unable to sample year-round in the ocean and thus had insufficient data to determine if there were seasonal changes or shifts in abundance.



FIGURE 67. Ocean densities of 0-age class Dungeness crabs collected by trawl, 1975–1979.

Bay vs. Ocean

Catch-per-unit-effort data were collected each autumn from 1975 through 1978 by trawling at selected Bay and Gulf stations. In 1975 and 1976 replicate 10-min trawls were made with the 8-ft beam trawl. In 1977 and 1978 we converted to a 43-ft otter trawl, reduced Bay station towing time to 5 min, and increased Gulf station towing time to 15 min. The frequency of occurrence of 0-age class crabs was determined for both study areas (Figure 68) and the CPUE (crabs per 10 min of trawling) was computed (Table 21).

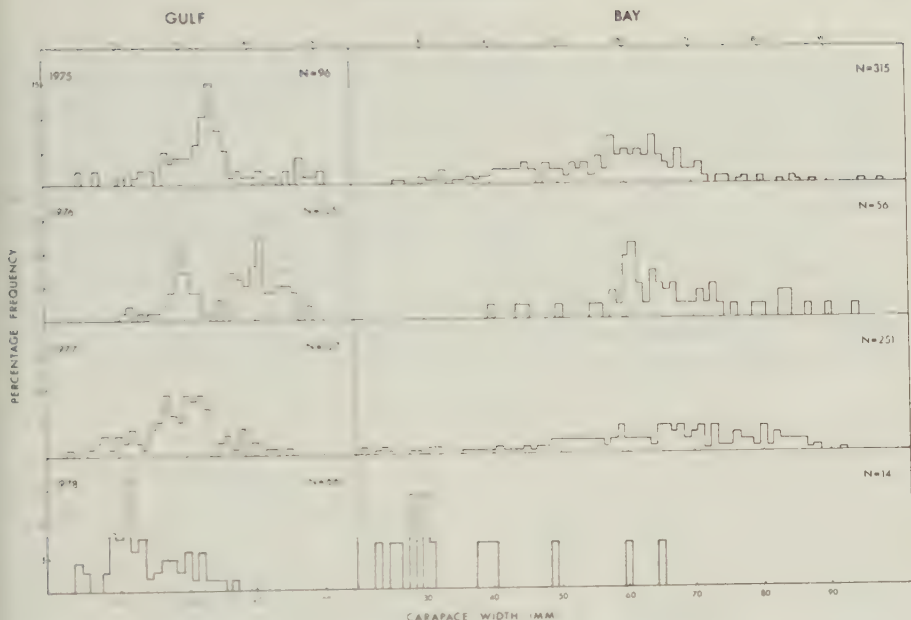


FIGURE 68. Frequency of occurrence of 0-age class crabs from autumn trawl collections, 1975-1978.

TABLE 21. Catch-per-unit-effort and Abundance Estimates for 0-Age Class Crabs, 1975-78.

	Gulf		Bay	
	CPUE (crabs/10-min trawl)	Abundance (millions)	CPUE (crabs/10-min in trawl)	Abundance (millions)
1975	2.7	2.0	12.6	9.3
1976	4.0	3.0	2.4	1.8
1977	4.0	1.0	26.4	5.9
1978	2.3	0.5	1.6	0.4

Abundance estimates (Table 21) were calculated using 500 km² of habitat for each area and escapement rates of 55%; surface area figures were from program collection data, preseason surveys (Walter Dalhstrom, Calif. Dep. Fish and Game, pers. commun.), and unpublished data (Richard Poole, Calif. Dep. Fish and Game). Diving surveys produced escapement rate data (Gotshall 1978a).

The years 1975 and 1977 appear to be the most successful in terms of total number of 0-age class crabs available for recruitment to the fishery (Table 21). The Bay contribution was approximately 83% during these years, but in 1976 and 1978 the figure dropped to 38%. Estimates of relative abundance derived from fish stomach data are similar only for 1975 (Bay = 77%) and 1978 (Bay = 42%). Bay contributions based on fish stomachs for 1976 and 1977 were 85% and 15%, respectively.

Growth

Data from the shore-based ringnet survey proved to be the most useful in analyzing growth parameters of 0-age class crabs. Monthly means of carapace widths (Table 22) for male crabs reared inside the Bay agree with those described by Collier (Chapter 9). A three-way analysis of variance on carapace widths was carried out on a subset of collection data with year class, sex, and month of the year as factors. All of the factors were found to be highly significant ($P \leq 0.0001$). A multiple classification analysis showed the following: (i) male crabs were larger than female crabs; (ii) 1977 year class crabs had the greatest widths, followed by the 1979 year class; (iii) 1978 year class crabs were the smallest. The difference in size between males and females was significant for each year of the study beginning about October (Figure 69).

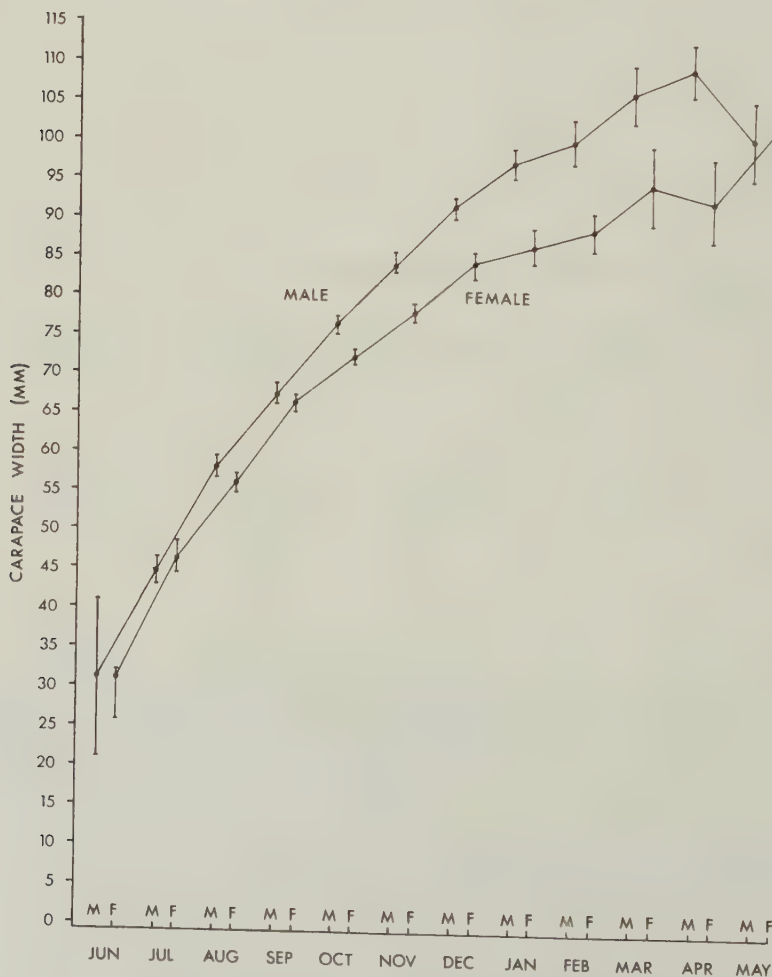


FIGURE 69. Growth rates of male and female crabs from shore-based ringnet survey, 1977-1980. Graph shows monthly means and 95% confidence intervals.

TABLE 22. 0-Age Class Dungeness Crabs from Shore-based Ringnet Survey, 1977-1980.

Year class	JUN		JUL		AUG		SEP		OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		Total
	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	N	$\bar{x}_{CW}$ (mm)	
1977-78																									
Male	5	51.8	73	47.7	295	60.7	278	69.6	345	78.1	398	85.9	488	92.3	248	98.0	101	99.3	52	106.7	64	109.3	47	101.7	2394
Female	5	31.2	70	48.2	248	59.3	300	67.8	362	74.1	278	80.0	313	85.3	93	88.0	43	89.9	17	94.4	10	92.0	8	101.4	1747
North Bay	10	41.5	118	49.9	330	63.6	434	69.7	518	77.2	599	89.4	746	90.7	290	75.9	96	96.1	49	104.3	60	107.1	44	104.2	
Central Bay	-	-	-	-	86	64.5	87	69.0	135	75.1	52	81.0	4	82.0	34	93.4	37	98.3	11	107.5	4	113.0	5	108.6	
South Bay	-	-	25	38.7	127	47.8	57	60.0	54	67.8	25	67.0	51	76.5	18	89.1	11	93.5	9	95.1	10	103.5	6	92.5	
1978-79																									
Male	-	-	-	-	12	45.1	34	54.5	76	66.2	79	74.2	25	75.1	58	89.6	40	96.0	47	101.3	58	113.1	-	-	429
Female	-	-	1	36.0	9	43.9	43	54.8	100	62.3	70	69.0	34	72.2	33	82.3	42	89.6	48	91.8	23	109.1	-	-	403
North Bay	-	-	1	36.0	2	47.0	24	55.5	53	71.5	75	77.2	27	75.9	81	87.4	58	95.9	59	98.8	80	112.1	-	-	
Central Bay	-	-	-	-	19	44.3	53	54.2	123	60.8	71	75.6	28	68.9	8	83.5	23	85.1	34	92.0	1	98.0	-	-	
South Bay	-	-	-	-	-	-	-	-	-	-	3	82.3	4	88.8	2	98.0	1	99.0	2	105.0	-	-	-	-	
1979-80																									
Male	-	-	49	49.3	302	52.04	477	63.5	204	69.4	114	80.5	117	82.9	92	91.8	13	94.7	32	94.8	-	-	-	-	1400
Female	-	-	46	40.7	449	51.5	572	62.9	301	65.5	119	76.8	91	81.0	50	86.6	6	84.8	20	87.1	-	-	-	-	1654
North Bay	-	-	95	42.1	185	50.0	297	61.4	165	70.9	164	78.4	180	85.4	138	90.1	11	93.2	1	76.0	-	-	-	-	
Central Bay	-	-	-	-	554	52.6	695	64.3	320	65.1	59	79.3	9	82.1	3	91.7	5	94.4	51	92.1	-	-	-	-	
South Bay	-	-	-	-	12	48.0	57	58.2	20	67.6	10	78.1	19	88.8	1	74.0	3	81.0	-	-	-	-	-	-	

Size differences also appeared between sampling areas. A one-way analysis of variance showed that the effect of location on mean carapace width is highly significant ($P \leq 0.0001$ for 1977 and 1978 year classes; $P \leq 0.001$ for 1979 year class). A priori multiple contrasts for north, central, and south Bay showed all pairwise mean differences to be highly significant for 1977 and 1978 year classes ($P \leq 0.01$), with north Bay crabs largest followed by central Bay and south Bay, respectively. In 1979 these contrasts show that only the north Bay mean was different from the central Bay mean. The other two pairing contrasts were not significant (each $P \leq 0.3$).

0-age class crabs caught by trawl in the Gulf were found to be substantially smaller than those collected in the Bay (Figures 68 and 70). Carapace width data show that it takes Gulf-reared crabs approximately 2 years after metamorphosis to the first post-larval instar to reach a size (ca. 100 mm cw) normally associated with the onset of sexual maturity. The average Bay-reared crab achieves this size within 1 year of settling. Carapace width frequencies of crabs collected in other Gulf studies (Walter Dahlstrom, Calif. Dep. Fish and Game, unpublished data) and from Bodega Bay (Richard Poole, Calif. Dep. Fish and Game, unpublished data; Wickham et al. 1976), compare favorably to ours. Wickham (Univ. Calif. Bodega Marine Laboratory, pers. commun.) found that crabs collected recently within Humboldt Bay also are larger, by an as yet undetermined percentage, than their year-class counterparts caught in the ocean.

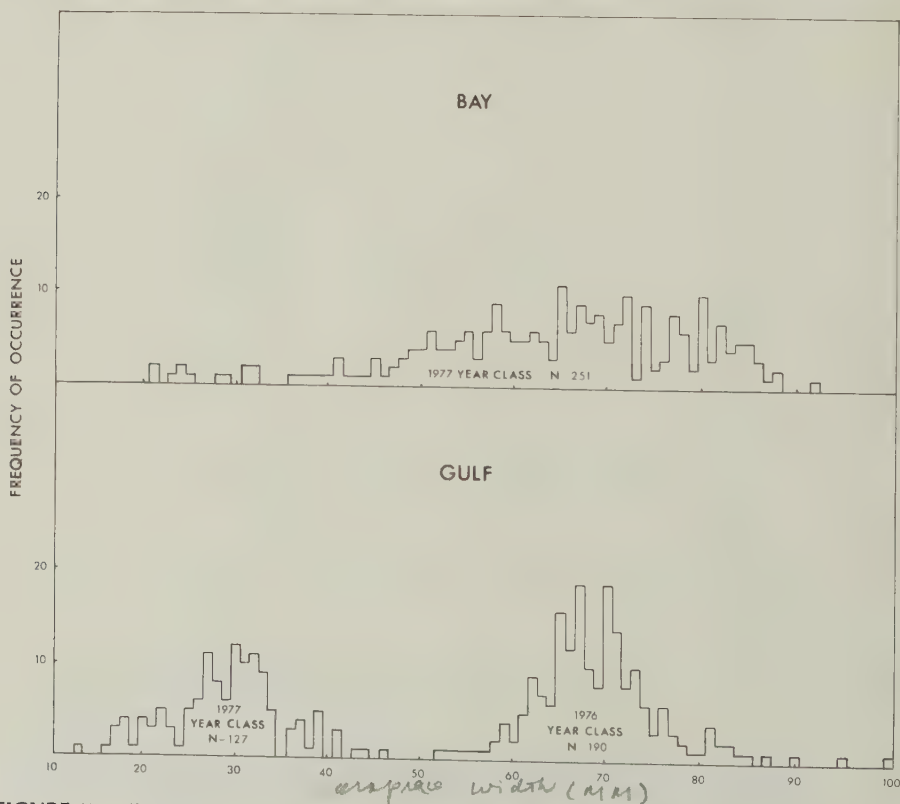


FIGURE 70. Frequency of occurrence of 0-age class crabs, autumn trawl collections 1977.

Historical data on juvenile crabs are limited. Dungeness crabs were collected in San Francisco Bay by the ALBATROSS survey 1912–13 and are repositied at the United States National Museum in Washington D.C. Carapace width data from that survey and from miscellaneous collections in the Bay during 1952–53 (curated at the California Academy of Sciences) were supplied by Daniel Wickham, University of California, Bodega Marine Laboratory. Carapace width measurements of crabs from San Francisco Bay generally agree with the sizes of Gulf-reared, 0-age class crabs from our study for similar time periods. Sizes of a small number from San Pablo Bay during 1952–53 compare more favorably to Bay-reared crabs from our study. Exact locations and methods of collection for these specimens are unreported.

Sex Ratios

Of 8,027 Dungeness crabs collected during the Bay shore-based ringnet survey (Table 22), 52.5% were male and 47.4% female. Females were most frequent during only 11 of the survey's 36 months; however, only 3 of these 11 months occurred during the 6-month periods following onset of the rainy seasons (November). In September, females outnumbered males for all 3 years of the survey and males likewise for January and March. Ringnetting from boats during October to March 1975 to 1978 in San Pablo and central San Francisco Bays yielded 1,248 (63%) males and 733 (37%) females. Trawl efforts during this period produced 555 (58%) males and 401 (42%) females.

Ocean caught 0-age class crabs showed a ratio of 1,107 (65%) males to 596 (35%) females. For all year classes caught by trawl in the ocean, the ratio was 1,940 (58%) males to 1,421 (42%) females.

Food Habits

Size differences between Gulf- and Bay-reared crabs, and within the Bay itself, prompted an abbreviated study in autumn and winter 1979 on food habits of juvenile Dungeness crabs. We collected specimens during our shore-based ringnet survey and by trawling. During September we retained 233 crabs. Also that month 76, 1-year-old crabs (51–90 mm cw) were caught by ringnet from Pacifica Pier (a fishing facility in the southern Gulf). In November, we ringnetted successfully in north and central Bay, collected only three crabs in south Bay, and were unable to catch any crabs off Gulf piers. For 2 days in December we trawled in central and north bay and captured 95 crabs. A shortage of crabs in January brought a halt to the study.

Stomach fullness was graded on a scale of 0 (empty) to 5 (full to capacity). In September, north and central Bay crabs averaged 3.0 and 2.9 (approximately half full), respectively, whereas south Bay and Gulf crabs were both 2.3. November figures were 2.4 for north and central Bay. Bay trawl-caught crabs in December averaged 3.3, but the figure for 13 north Bay ringnet-caught crabs in January was 2.6.

The frequent occurrence of skeletal remains of fish and crustaceans and shells of bivalves implies that food items are captured alive. The live state and type of food items ingested agree with determinations by MacKay (1931), Cleaver (1947), Butler (1954), Gotshall (1977), and Bernard (1979). Frequency of occurrence data (Table 23) indicate that fish are more available as food items

TABLE 23. Frequency of Occurrence of Food Items from 583 Dungeness Crab Stomachs Collected by Ringnet (R) and Trawl (T), 1979-80.

Items	North Bay				Central Bay			South Bay		Gulf
	Sep (R) (N=81)	Nov (R) (N=105)	Dec (T) (N=92)	Jan (T) (N=13)	Sep (R) (N=72)	Nov (R) (N=58)	Dec (T) (N=3)	Sep (R) (N=80)	Nov (R) (N=3)	
POLYCHAETES										
<i>Nereis procera</i>		1								
MOLLUSKS										
Squid (bait)	36	23			29	10		28		
Bivalve parts										
(shell, muscle, siphon, etc.)	6	19	80	2	7	12		7		5
<i>Mytilus</i>	5	29		4	8	3				
CRUSTACEANS										
Carideans			6							
Barnacles										
(shell fragments)		1	1		4	4	1			4
Isopods	3	5	48		1	1		2		1
Amphipods			3					1	1	
Gammarid amphipods										
Caprellid amphipods			1					2		
<i>Cragon franciscorum</i>					1			1		
Crab carapace fragments	1	6	1		6	16	1	1		4
<i>Cancer antennarius</i>										1
<i>Cancer gracilis</i>										1
OPHURIIDS						1				1
CHORDATES										
Ascidian (solitary)								1		
Fish remains (vertebrae, scales, spines, etc.)	2	7	6	4		4			1	43
MISCELLANEOUS										
Unrecognizable muscle		18								2
Algae	1	12	7	1	2	2	1	1		1
Detritus	33	71	40	10	36	47	1	51	1	61
Unidentified	8	1			6			1		
Empty	6	8			4	1	1	10		2

to Gulf crabs and crustaceans and bivalves to Bay crabs. No differences appear between areas within the Bay for food item types, but the stomach fullness index indicates that more food is available in north and central Bay than in south Bay, as well as the Gulf. Trawling proved to be the best method for collecting crabs for food habit analysis. According to Gotshall (1977), trawling at night improves the catch and proportion of full stomachs.

DISCUSSION

Observations of the behavior and distribution of megalopae (Reilly, Chapter 6; Hatfield, Chapter 7), coupled with the distributional pattern of early stage post-larval instars, indicate that bottom current is the likely mechanism for the entrance of Dungeness crabs into the Bay in May and June. Conomos et al. (1971) determined through the use of seabed drifters that the net flow of bottom water from areas west of and adjacent to the Golden Gate is into the estuary, principally central and north Bay (Figure 71). The number of crabs entering the Bay fluctuates from year to year, depending primarily on numbers of megalopae arriving in the nearshore area and possibly on the strength of bottom currents.

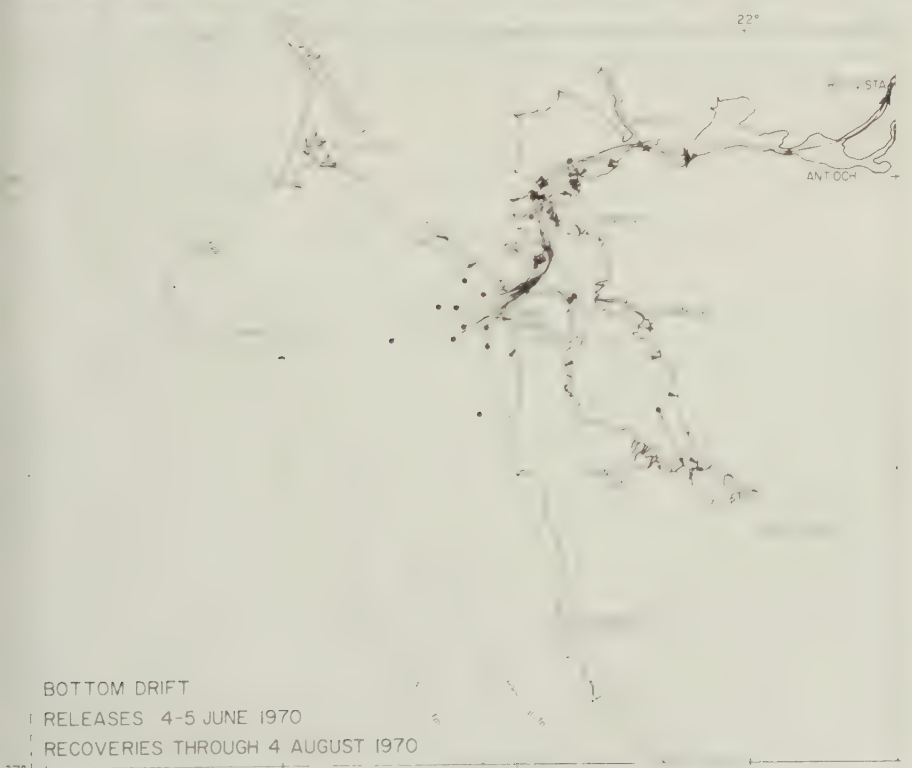


FIGURE 71. Release and recovery points for seabed bottom drifters. Illustration from Conomos et al. (1971).

By autumn, the crabs' increased size and mobility dictate distributional patterns based on food supply, habitat, and environmental factors such as temperature and salinity. Piers, jetties, boat launching facilities, and other structures that offer protection and are a possible source of food items attract crabs in larger numbers than exposed areas.

The cause of the faster rate of growth in Bay-reared crabs as opposed to ocean-reared crabs is not completely clear. Temperature probably is an important factor, for overall Bay temperatures averaged about 5 C higher than ocean temperatures. However, north Bay, which generally has larger crabs than central or south Bay, exhibited slightly colder temperatures than south Bay (Figure 72). It may also be reasoned that crabs enter the south Bay as a result of later settling, although we have no evidence of this. Early instar crabs coming into the Bay in June when Delta outflow generally is reduced may be subjected to less forceful bottom currents and, as a result, have a better chance of being distributed into south Bay. Belated settling would subsequently appear in smaller monthly carapace width averages for south Bay crabs. Salinities generally are lower in north Bay than in either central or south Bay (Figure 73) and, over the year, average less than those recorded in the ocean. Yet it is difficult to explain how such differences in salinity could directly account for the varying growth rates. The seemingly greater availability of food items in the Bay, particularly crustaceans, may be a factor.

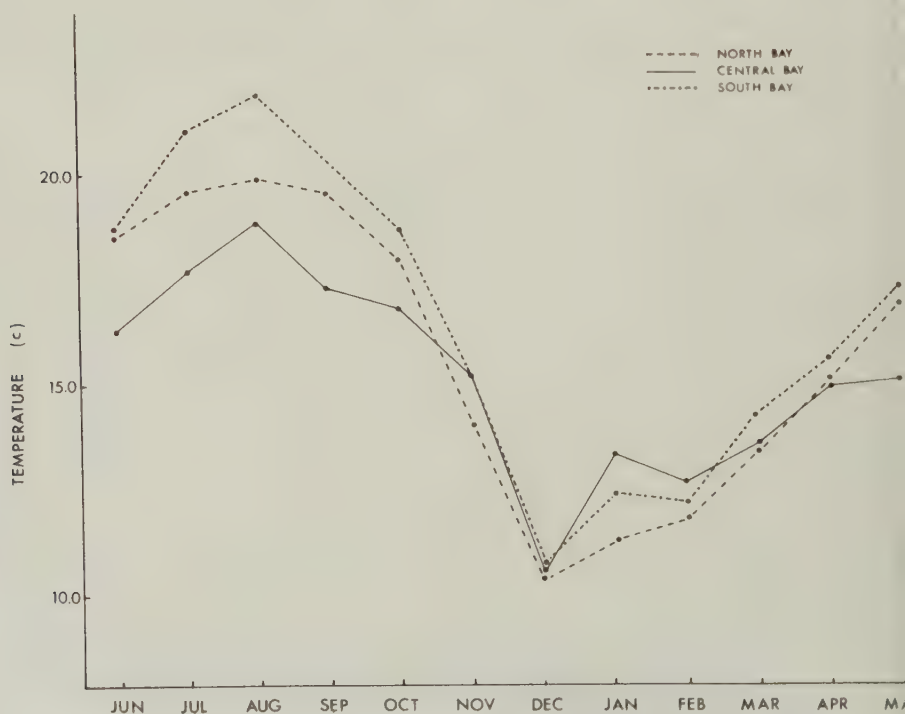


FIGURE 72. Average monthly temperature variations during shore-based ringnet survey 1977-1980.

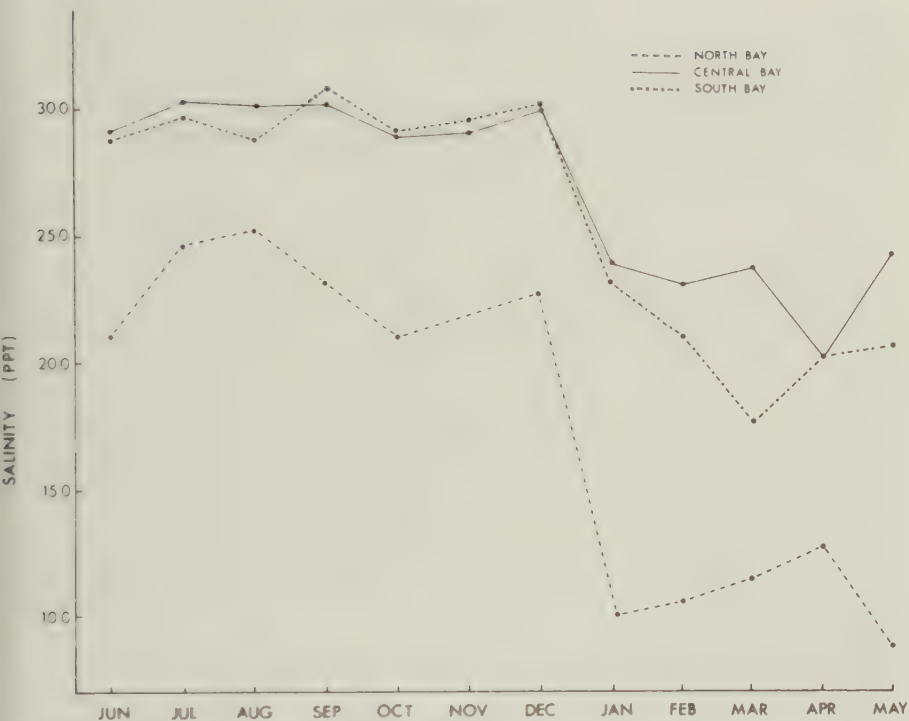


FIGURE 73. Average monthly salinity variations during shore-based ringnet survey, 1977–1980.

The significance of the accelerated growth rate in Bay-reared crabs is speculative. Botsford (1981) states that this increased rate is symptomatic of an exploited, unstable population or one that has been subjected to less than 10% recruitment for a number of successive years. He continues by saying that the population achieves a lower, more stable equilibrium in which the larger individuals, beneficiaries of the new rates, are involved in an inter-age, density-dependent function which adds to the depressed state. He does not take into account that ocean-reared crabs in the San Francisco fishery do not experience this high rate of growth.

It has been generally reported (PFMC 1979) that male and female growth rates are comparable until sexual maturity (ca. 93–108 mm cw) is reached. My study shows that rates for San Francisco Bay-reared male and female crabs diverge earlier. Future research should attempt to determine if sexual maturity is achieved at a smaller size in Bay-reared crabs.

Reductions in salinity due to freshwater runoff cause changes in crab distribution. The crabs appear to consolidate in certain areas (salinity > 10 ppt). Cleaver (1949) reports that laboratory held adult crabs can tolerate salinities as low as 11 ppt, but those in Gray's Harbor, Washington "seemed to retreat before a freshet."

This consolidation may be interpreted as a mobilization. Movement out of the Bay (Collier, Chapter 9) probably is a function of size, as evidenced by a drop

in mean carapace width for crabs collected in May. It is likely that the majority of crabs move toward the center of the Bay in response to freshwater input and, after reaching a certain size range, begin to emigrate. Peak movement occurs during April–May and, by the end of summer, movement and mortality account for the loss to the Bay of most ($> 90\%$) of the outgoing year class. The new year class becomes established in May–June.

The distribution of 0-age class crabs in the ocean off central California is somewhat of an enigma. There appears to be a substantial amount of suitable substrate that is not being utilized. Daniel Gotshall (Calif. Dep. Fish and Game unpublished manuscript) reports the capture of large numbers of juveniles on “green mud” in 50 to 100 fathoms (90 to 180 m) off Eureka and Crescent City. The locations of 0-age class crab concentrations in the Gulf and ocean north to Bodega Bay appear to be a result of ocean currents that distribute megalopae. These currents distribute most of the megalopae in an area along the coast from Drake’s Bay to Bodega Bay. Year to year fluctuations in juvenile crab abundance noted in Bodega Bay (Poole 1966; Wickham et al. 1976) are less obvious in the Gulf, particularly by autumn following several months of predation. The shallow, sandy stretches just south of the shipping lanes southwest of the Golden Gate provide a staging area for 1-year-old juvenile crabs that exit the Bay during spring and early summer (Walter Dahlstrom, Calif. Dep. Fish and Game, pers. commun.). Effects of predation by these crabs on newly settled megalopae or early post-larval instars has not been ascertained.

The higher percentage of males collected over the course of the study is difficult to understand. Aggressiveness and larger size of males may account for their superiority in numbers in crab traps and ringnets. In addition, early post-larval instars are not as easily sexed as later instars and this may explain some of the disparity in the trawl data. There are, however, other sets of data, notably trawl efforts in San Pablo Bay in autumn and winter when crabs are easily sexed but in which males still predominate. Unlike crab traps, trawl catches should not be affected by size and aggressiveness. The relevance of these differences needs to be investigated.

I feel that as a result of this study we have established the current high value of San Francisco Bay as a Dungeness crab nursery ground. The contribution the Bay makes to local recruitment appears to be directly proportional to megalopal year-class strength (Reilly, Chapter 6). Inadequate historical data exist with which to compare the current situation, as we find it, to the period when commercial landings were high. Weymouth (1916) indicates that in the late 1800’s Dungeness crabs were found in abundance between San Francisco and the Golden Gate but that by 1913 they had all but disappeared; however, no sizes or sex ratios are given. Such meager references are of little value and we are left to speculate on what effect that changes in the Bay such as landfill, regulated Delta outflows, etc. may have had on commercial landings.

Chapter 11

PREDATION ON DUNGENESS CRABS, *CANCER MAGISTER*, IN CENTRAL CALIFORNIA

by

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INTRODUCTION

Several studies document predation on Dungeness crabs, *Cancer magister*, by various demersal fishes (Waldron 1958; Gray 1964; McKechnie and Fenner 1971; Prince and Gotshall 1976) and invertebrates (Butler 1954; Waldron 1958; Gotshall 1977; Van Veldhuizen 1978). References to crab megalopae as prey items for king and silver salmon, *Oncorhynchus tshawytscha* and *O. kisutch*, in the northeastern Pacific are numerous. Dungeness crab megalopae have been identified in some of these references (Heg and Van Hyning 1951; Merkel 1957; Prakash 1962; Gunsolus 1978), while others only report the occurrence of *Cancer* sp. megalopae in salmon stomachs (Silliman 1941; Pritchard and Tester 1944; Petrovich 1970).

I used demersal and pelagic fishes as biological samplers to obtain data on growth, distribution, relative year-class strength, and mortality of Dungeness crabs in central California and compared these with data collected by conventional methods. My purpose was to determine whether mortality from predation could be related to the decline and continued low level of the commercial crab fishery in central California (Figure 10). Studies of predation on megalopae by pelagic fishes were limited to king and silver salmon.

METHODOLOGY

Demersal and pelagic fishes were collected in the Gulf of the Farallones (Figure 11) and the San Francisco-San Pablo-Suisun Bay complex (Figure 12) from April 1975 to May 1979 during the months March to June, September, and October. In May 1979, we extended our sampling to the Pt. Reyes-Bodega Bay area (Figure 17). We used several types of gear: (i) an 8-ft (2.4-m) beam trawl with a 1.25-inch (32-cm) mesh and a 0.5-inch (1.3-cm) mesh liner in the cod end; (ii) a 16-ft (4.8-m) or 43-ft (13-m) otter trawl with mesh similar to the beam trawl; and (iii) hook and line. Stomachs were also collected from commercially caught king and silver salmon, primarily from the Gulf, but some to 65 km north of Pt. Reyes. In April 1980, we chartered a commercial salmon troller to collect data on megalopal predation by salmon and to conduct plankton tows concurrently in nearshore waters off Fort Bragg (Figure 18).

Each fish retained for analysis was measured (total length) and its stomach and intestinal tract were removed, wrapped in cheesecloth, and placed in a 10% formalin solution. The following data were recorded: station number, date, time, station depth, and, in trawl samples, counts of associated fish and invertebrate

species. In the laboratory, stomachs and intestinal tracts were opened and the contents placed in a water-filled dissecting tray. Recognizable food items were examined under a binocular microscope and identified to the lowest taxon possible. When sufficiently intact, post-larval Dungeness crabs were measured for carapace width (cw), excluding 10th anterolateral spines, and sexed; all were retained in 50% isopropyl alcohol solution.

RESULTS AND CONCLUSIONS

From 1975 to 1980, stomachs of 1,537 ocean-caught demersal fishes from the Gulf and Bodega Bay-Pt. Reyes area were examined; of these, 1,170 contained recognizable food items. In 249 stomachs containing Dungeness crab material, we found 995 megalopae, 1,385 young-of-the-year post-larval instars, and 7 older-year-class crabs. We examined 1,061 stomachs from Bay-caught fishes, of which 889 contained recognizable food items; 122 stomachs containing Dungeness crabs yielded 4 megalopae, 361 young-of-the-year, and 7 older-year-class crabs. During March to June, 1977 to 1980, we examined 45 king and 40 silver salmon stomachs from ocean waters between Fort Bragg and the Gulf. These yielded 132 and 1,196 megalopae, respectively.

Of seventy species of fishes examined for stomach contents, we found 28 to have preyed upon Dungeness crabs (Appendix VII). The most important predators, based on the frequency of occurrence and number of crabs per stomach, were silver and king salmon; starry flounder, *Platichthys stellatus*; English sole, *Parophrys vetulus*; rock sole, *Lepidopsetta bilineata*; brown smoothhound, *Mustelus henlei*; big skate, *Raja binoculata*; Pacific tomcod, *Microgadus proximus*; Pacific staghorn sculpin, *Leptocottus armatus*; white croaker, *Genyonemus lineatus*; pile perch, *Damalichthys vacca*; and green sturgeon, *Acipenser medirostris*.

Predation by Salmon

Twelve stomachs from commercially-caught silver salmon collected in early May 1977 from the Gulf indicate that this predator has the potential to cause significant mortality during the megalopal stage; eight of the stomachs contained a total of 1,061 megalopae. During May and June 1978, 14 stomachs were examined from silver salmon collected in the Gulf; one stomach contained two megalopae. The disparity between these years reflects relative strengths of larval year classes (Reilly, Chapter 6).

Most of the king salmon stomachs examined from Gulf stations were collected in March 1978 and no megalopae were found in these. The absence of megalopae was most likely due to their absence from the plankton in the study area. Megalopae were absent in all 144 Gulf plankton samples during our March cruise but occurred at low densities in April.

In April 1980, we studied the relationship between salmon predation on megalopae and megalopal abundance in the plankton. We trolled 39 hr for salmon during April 2-4 and 14-17 near Fort Bragg and we took 43 surface and 18 oblique plankton tows, the latter to depths of approximately 25 m. The first 3 days yielded no megalopae in plankton samples but 68 megalopae were taken from three of six silver salmon stomachs. Either megalopae were preyed upon outside of the sampling area which ranged from 1 to 11 km from shore, or

megalopal density in the plankton was so low that our tows did not collect any. During the April 14–17 sampling, two silver salmon stomachs contained a total of 63 megalopae and nine king salmon stomachs contained a total of 131 megalopae. Average densities of megalopae in surface and oblique tows were 0.3 and 0.2/100 m³ of water, respectively.

A direct relationship was evident in the data from 1977 and 1980 between abundance of megalopae in plankton samples and frequency of occurrence as prey items for salmon. Both were much more abundant in 1977 than in 1980.

It appears that salmon may feed selectively on Dungeness crab megalopae as well as certain other members of the plankton community. Dungeness crab megalopae were the most frequently occurring prey item in the 1980 king salmon stomach samples and the second most abundant item after the pelagic gastropod, *Limacina* sp., in silver salmon stomachs. Zoeae of the sand crab, *Emerita analoga*, were 38 times more abundant than Dungeness crab megalopae in oblique tow samples, but occurred less frequently than megalopae in the silver salmon stomachs, and not at all in the king salmon stomachs. Salps, fish eggs, and anomuran zoeae were also common in plankton tows, but absent in stomach contents, while the heteronereid form of the polychaete *Nereis procera* and megalopae of the sand crab, *E. analoga*, were noticeably more common in stomach contents than in plankton samples.

Predation by Demersal Fishes

The occurrence of megalopae and young-of-the-year post-larval instars in stomachs of demersal fishes (Figure 74) indicates that settling by megalopae and molting to the juvenile stage occurs primarily in the nearshore area. Megalopae were found in fish stomachs to a depth of 60 m. However, of 995 megalopae collected, 965 occurred at stations with depths less than 25 m and within 10 km of shore. All but two of 1,385 young-of-the-year crabs from demersal ocean fishes occurred within 8 km of shore. A large proportion of these were in the first post-larval instar. First post-larval instar Dungeness crabs average approximately 7 mm carapace width (cw) (Collier, Chapter 9) and often are missed in trawl samples. Demersal fishes are more efficient in capturing this stage. In May 1977, 5 hours of trawling yielded only one Dungeness crab less than 8 mm cw, while examination of 135 fish stomachs from the same stations yielded 746 crabs of similar size. The distribution of early post-larval instars from fish stomachs appeared more clumped in the ocean, thus increasing their vulnerability to predation. For example, the maximum number of young-of-the-year crabs observed in one stomach of the starry flounder was 237 in the Gulf; a maximum of 10 was observed in a Bay-caught starry flounder.

Relative strengths of Dungeness crab year classes from 1975 to 1979 were compared by examining predation data from the Gulf and the Bay (Tables 24 and 25). In 1977 and 1979, the average number of crabs per stomach was higher in ocean waters than in the Bay. The data indicate that a relatively strong set of juvenile crabs occurred in 1977, correlating well with the relatively high abundance of megalopae in plankton tows taken during April 1977 (Reilly, Chapter 6; Table 9), and that the years 1975 and 1979 also were relatively good for recruitment of juvenile crabs to the Gulf and the Bay.

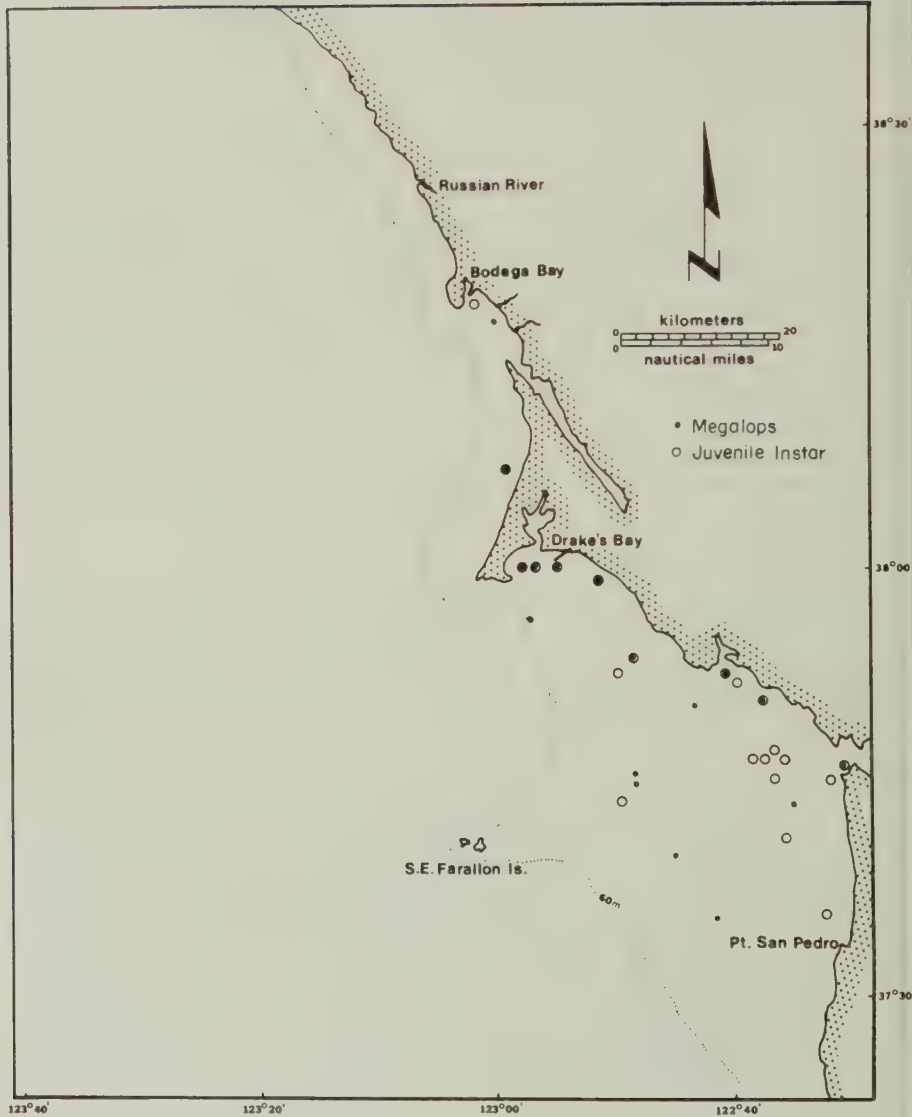


FIGURE 74. Distribution of megalopae and post-larval young-of-the-year Dungeness crabs in demersal fish stomachs from Bodega Bay to Pt. San Pedro, 1975–1979.

TABLE 24. Occurrence of Post-larval, Young-of-the-year Dungeness Crabs in Fish Stomachs from the Gulf of the Farallones (A = Number of Stomachs Examined with Food; B = Number of Stomachs Containing Dungeness Crabs; C = Total Number of Dungeness Crabs in Stomachs; D = Average Number Per Stomach).

Predator	1975				1976				1977				1978				1979*			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
<i>Acipenser medirostris</i>	-	-	-	-	-	-	-	-	1	1	53	53.0	-	-	-	-	-	-	-	-
<i>A. transmontanus</i>	-	-	-	-	-	-	-	-	1	1	36	36.0	-	-	-	-	-	-	-	-
<i>Damalichthys vacca</i>	1	0	0	0.0	-	-	-	-	3	1	1	0.3	-	0	0	-	-	-	-	-
<i>Genyonemus lineatus</i>	5	0	0	0.0	6	1	1	0.2	28	7	20	0.7	16	1	2	0.1	2	0	0	0.0
<i>Hexagrammos decagrammus</i>	-	-	-	-	2	0	0	0.0	4	1	35	8.7	-	-	-	-	-	-	-	-
<i>Lepidopsetta bilineata</i>	-	-	-	-	2	0	0	0.0	5	5	60	12.0	3	0	0	0.0	1	0	0	0.0
<i>Leptocottus armatus</i>	4	0	0	0.0	-	-	-	-	17	7	9	0.5	11	2	2	0.2	-	-	-	-
<i>Microgadus proximus</i>	-	-	-	-	3	0	0	0.0	20	4	6	0.3	14	2	4	0.3	31	19	91	2.9
<i>Mustelus henlei</i>	-	-	-	-	-	-	-	-	6	3	7	1.2	2	0	0	0.0	2	0	0	0.0
<i>Parophrys vetulus</i>	7	0	0	0.0	10	0	0	0.0	23	6	75	3.3	14	0	0	0.0	9	2	37	4.1
<i>Platichthys stellatus</i>	12	1	6	0.5	10	0	0	0.0	31	15	840	27.1	28	1	1	0.04	6	2	4	0.7
<i>Raja binoculata</i>	9	0	0	0.0	9	0	0	0.0	17	8	91	5.4	9	2	2	0.2	-	-	-	-
<i>Rhacochilus toxotes</i>	2	1	2	1.0	-	-	-	-	1	0	0	0.0	-	-	-	-	-	-	-	-
TOTALS	40	2	8	-	42	1	1	-	157	59	1233	-	98	8	11	-	51	23	132	-

*Includes data from Pt. Reyes-Bodega Bay area

TABLE 25. Occurrence of Post-larval, Young-of-the-year Dungeness Crabs in Fish Stomachs from the San Francisco Bay Estuarine Complex (A = Number of Stomachs Examined with Food; B = Number of Stomachs Containing Dungeness Crabs; C = Total Number of Dungeness Crabs in Stomachs; D = Average Number Per Stomach).

Predator	1975				1976				1977				1978				1979			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
<i>Acipenser medirostris</i>	1	1	6	6.0	-	-	-	-	4	2	40	10.0	-	-	-	-	-	-	-	-
<i>Damalichthys vacca</i>	-	-	-	-	1	0	0	0.0	17	7	36	2.1	4	0	0	0.0	1	0	0	0.0
<i>Gemyonemus lineatus</i>	6	2	5	0.8	10	1	1	0.1	30	7	16	0.5	24	2	2	0.1	4	1	1	0.2
<i>Leptocottus armatus</i>	34	11	28	0.8	12	1	2	0.2	32	15	20	0.6	15	1	1	0.1	1	0	0	0.0
<i>Microgadus proximus</i>	3	0	0	0.0	-	-	-	-	11	0	0	0.0	17	0	0	0.0	8	1	1	0.1
<i>Mustelus henlei</i>	5	3	15	3.0	10	1	2	0.2	49	26	94	1.9	37	3	3	0.1	4	1	2	0.5
<i>Myliobatis californica</i>	-	-	-	-	-	-	-	-	2	1	1	0.5	-	-	-	-	-	-	-	-
<i>Parophrys vetulus</i>	3	0	0	0.0	-	-	-	-	3	1	1	0.3	-	-	-	-	3	0	0	0.0
<i>Phanerodon furcatus</i>	1	0	0	0.0	1	0	0	0.0	4	1	1	0.2	-	-	-	-	2	0	0	0.0
<i>Platichthys stellatus</i>	48	6	11	0.2	16	0	0	0.0	28	4	22	0.8	15	1	1	0.1	5	1	1	0.2
<i>Raja binoculata</i>	1	1	1	1.0	1	0	0	0.0	17	12	44	2.6	11	2	2	0.2	1	0	0	0.0
<i>Triakis semifasciata</i>	-	-	-	-	1	1	1	1.0	7	0	0	0.0	1	0	0	0.0	-	-	-	-
TOTALS	100	24	66	-	52	4	6	-	193	76	275	-	107	9	9	-	29	4	5	-

Carapace width frequencies of juvenile crabs found in fish stomachs (Figure 75) show that the first post-larval instar was a more common prey item in the Gulf than in the Bay. This suggests that many young-of-the-year crabs enter the Bay after molting to the second instar.

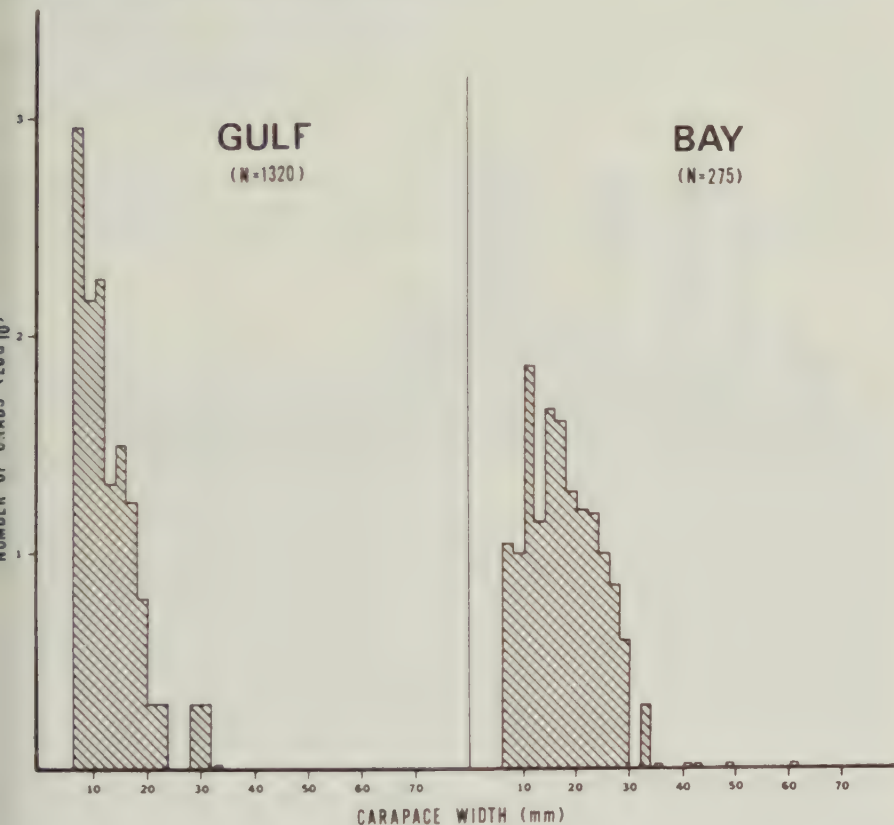


FIGURE 75. Carapace width frequency distributions (2-mm intervals) of post-larval young-of-the-year Dungeness crabs found in demersal fish stomachs, 1975-1979.

The predation data (Figure 75) show a slower growth rate for crabs in the Gulf compared to the Bay, a condition also reported by Collier (Chapter 9) and Tasto (Chapter 10). In mid-April 1977, all young-of-the-year crabs in stomachs of fishes from Gulf stations were megalopae or first instars. Most crabs ranged from 8 to 12 mm CW in May, 10 to 18 mm in June, and 14 to 33 mm in September. In the Bay, crabs ranged from 8 to 23 mm CW in May, 14 to 44 mm in June, and 19 to 60 mm in September. The faster growth rate in the Bay allows young-of-the-year crabs to reach a size less vulnerable to predation by September. Most crabs collected during trawling and ringnetting in the Bay exceeded 40 mm CW in September (Collier, Chapter 9), and predation was observed less frequently than in the Gulf where the majority of young-of-the-year crabs caught in trawls ranged from 15 to 40 mm CW (Robert N. Tasto, pers. commun.). Growth data

for crabs from fish stomachs in 1975 and 1977 were similar; sample sizes were too small to analyze in the other years (Tables 24 and 25).

I estimated natural mortality for young-of-the-year Gulf crabs between May and September 1977, based on the average number of crabs per predator stomach at those stations where crabs occurred. For May, June, and September, average numbers of crabs per stomach were 24.0, 2.2 and 0.5, respectively, an overall decline of approximately 98% during the 4-month period. Thus, the potential mortality of a year class due to predation is substantial and is exemplified by the occurrence of 769 juvenile crabs in 12 Gulf-caught starry flounder stomachs.

Predation continued to be a factor of natural mortality during periods of molting throughout the life of the crab. We found crabs up to 150 mm cw in fish stomachs which apparently had been preyed upon when their exoskeletons were soft.

DISCUSSION

Biological samplers are often more efficient than conventional sampling methods in capturing larval and early post-larval stages of prey items (Gotshall 1969; Reilly and Sails 1978). Merkel (1957) examined 1,004 king salmon stomachs collected from the Gulf and the Bay in 1954 and 1955 and found a total of 10,800 Dungeness crab megalopae in 107 of them; all occurred from March to July with only a few being found after May. During 1948–1950, Heg and Van Hyning (1951) examined stomachs of 319 silver and 125 king salmon from Oregon waters and found that when silvers were feeding heavily on Dungeness crab megalopae, predation by king salmon was substantially less. A similar relationship was observed off Washington in June 1938 for *Cancer* sp. megalopae (Silliman 1941); silver salmon had a greater average weight of megalopae per stomach than king salmon. Petrovich (1970) also noted that silver salmon consumed more *Cancer* sp. megalopae than king salmon off Humboldt Bay and Trinidad Head, California. We could not discern any major differences between the frequency of occurrence of Dungeness crab megalopae in king versus silver salmon stomachs in the Fort Bragg area during April 1980, probably because our sample size was too small.

The contribution of both of these pelagic, migratory coastal predators to the mortality of Dungeness crabs is undoubtedly significant. The production of king salmon, based on catch statistics, has not experienced a significant increase over the past two decades. However, an intriguing question arises when silver salmon production is considered. Between 1940 and 1960, silver salmon caught in California, Oregon, and southern Washington were predominantly wild fish and stocks were at low levels (Gunsolus 1978). Beginning in 1960, fish culture techniques improved at Columbia River hatcheries and increased numbers of healthy smolts were released to supplement the wild population. Annual releases ranged from 15.1 to 34.2 million during the period 1961 through 1976 (Gunsolus 1978). Mark and recapture studies show that the majority of silver salmon caught in California originated in streams and rivers of Oregon and Washington (Wahle et al. 1974; Johnson 1970; Patrick O'Brien, Calif. Dep. Fish and Game, Sacramento, unpublished manuscript). The Oregon Production Index is a measure of catch and escapement of Oregon and Columbia River silver salmon stocks (Gunsolus 1978). This production index includes fisheries in California, Oregon,

the Columbia River, and southern Washington. A dramatic increase occurred in Oregon (Gunsolus 1978) and California silver salmon landings (Figure 76) during the mid-1960's, following the decline of the central California Dungeness crab fishery by just a few years.

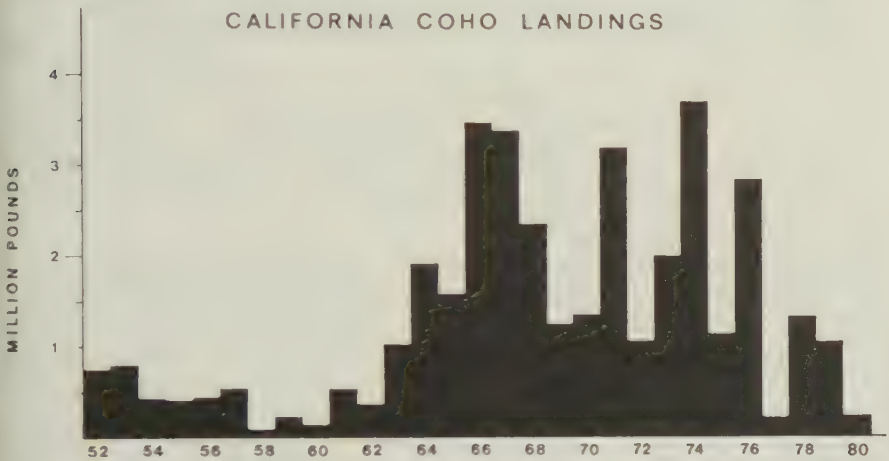


FIGURE 76. Silver (coho) salmon landings in California, 1952-1979.

An undetermined portion of the annual Columbia River hatchery production contributes substantially to salmon stocks found along the California coast (Dave Thomas, Calif. Dep. Fish and Game, unpublished manuscript). The spring arrival of Dungeness crab megalopae in nearshore ocean waters coincides with the northward migration of these fish. Our data show that silver salmon may prey heavily upon megalopae in the Gulf and probably intercept those being transported from the north.

The relationship between megalopae and silver salmon abundance in California requires further study. The collapse of the central California Dungeness crab fishery actually occurred prior to the increased hatchery production on the Columbia River considering the 3- to 4-year lag time required for crabs to reach legal size. The initial crab decline coincided with a significant warming trend in the California Current region and there is evidence that the decline may be related to that oceanographic change (Wild, et al., Chapter 14; Wild, Chapter 16). Nevertheless, there appears to be a direct relationship between silver salmon hatchery production in Oregon and the magnitude of predation on megalopae in California waters, and it may be that the increase in salmon production is at least partially responsible for the continued suppression of recruitment of larval crabs to the San Francisco area fishery.

Various studies demonstrate the importance of Dungeness crabs as a prey item of demersal fishes and invertebrates. Prince and Gotshall (1976) found Dungeness crab megalopae and post-larval instars to be the most important food items for the copper rockfish, *Sebastes caurinus*, in Humboldt Bay, California. Large crabs, up to 114 mm CW, have been consumed by the cabezon, *Scorpaenichthys marmoratus*, in Oregon waters (Waldron 1958) and the Pacific halibut, *Hippoglossus stenolepis*, off Alaska (Gray 1964). Waldron (1958) also lists

the wolf eel, *Anarrichthys ocellatus*, lingcod, *Ophiodon elongatus*, halibut, *H. stenolepis*, and various rockfishes, *Sebastes* [= *Sebastes*], as important predators of adult crabs, and crabs and octopuses as predators to a limited extent. Dungeness crabs comprised 32% by volume of the stomach contents of white sturgeon, *Acipenser transmontanus*, collected in San Pablo Bay during the fall from 1965 to 1967, less than 2% during winter and summer, and were not a food item in the spring (McKechnie and Fenner 1971). This demonstrates an increased availability to predators when the new year class is at maximum dispersion in the Bay complex during the fall (Tasto, Chapter 9). Van Veldhuizen (1978) reported predation on megalopae and early post-larval instar crabs by the starfish, *Pisaster brevispinus*, in Bodega Harbor. The cannibalistic nature of Dungeness crabs has been verified by studies in northern California (Gotshall 1977) and Oregon (Waldron 1958).

During our studies in 1977, only one first instar Dungeness crab was found in trawl samples while crabs of this stage were particularly abundant in fish stomachs. Catch-per-unit-effort trawl surveys in September 1977 (Tasto, Chapter 10) showed that approximately 83% of the juvenile crabs from the Bay and Gulf were caught in the Bay. However, during April to June 1977, the average number of crabs per stomach for all predatory species in the Bay and Gulf was more than five times higher in the Gulf. Evidently the clumped distribution of settling megalopae and the slower growth rate of juveniles in the Gulf constitute a less advantageous situation for survival than in the Bay, so that by September, substantial initial differences between crab abundance in the Gulf and the Bay may be negated or reversed. The nearshore, sandy habitat between Bodega Bay and Pt. San Pedro (Figure 65) generally is occupied by the incoming year class of juvenile crabs and also by several important predators, including starry flounders, English sole, and rock sole. We have no evidence that any species of nearshore or estuarine demersal predators of Dungeness crabs in central California experienced a substantial increase in population concurrent with the decline of the commercial crab fishery beginning in 1960–61. Therefore, it is unlikely that inherent natural mortality from demersal predators would have caused the significant decline and sustained low yield in the commercial fishery.

Our limited data on predation of Dungeness crab megalopae by silver salmon and the increase in Oregon silver salmon hatchery production, which has resulted in increased catches in California concurrent with the crab decline, demonstrate an area of critical concern which warrants further study.

Chapter 12

EFFECTS OF COMMERCIAL TRAWLING ON DUNGENESS CRAB SURVIVAL

by

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INTRODUCTION

Commercial trawl vessels operate from the same ports along the coast as commercial Dungeness crab boats, although trawling, unlike crabbing, is prohibited by law within 3 miles (4.8 km) of shore. During the commercial crab season, trawlers generally do not operate in crabbing areas outside the 3-mile limit because of the hazard presented to their gear by crab traps. By law, commercial trawlers in California may possess no more than 500 lb (227 kg) of crabs at a time during the open season and are prohibited from retaining them during the closed season. Only male crabs 159 mm or larger in carapace width (CW), excluding 10th anterolateral-spines, may be taken legally. During the closed season which currently is from July 1 to the 2nd Tuesday in November in central California, trawlers move into crabbing areas to drag for bottomfishes.

In central California, female Dungeness crabs molt primarily during the spring and early summer and males during summer and fall. Crabs are soft and defenseless immediately after molting and, as the crab's exoskeleton hardens, the flesh (or muscle) mass increases to fill out the new exoskeleton. These are known as "filling" crabs. Soft and filling crabs are more susceptible to injury than "hard" crabs. Concern over the impact of trawling on crabs, particularly during the closed season, prompted this investigation.

In 1980, we contracted with a commercial trawl boat operator so that we could conduct a study to determine magnitude and condition of Dungeness crab catches in trawls. Our objective was to estimate mortality caused by trawling operations in the Gulf of the Farallones (Figure 11) and to determine whether there is significant impact on the crab fishery in the San Francisco area.

METHODOLOGY

In July, August, and September 1980, we chartered the Bodega Bay dragboat SANIBEL to trawl in the Gulf of the Farallones. Trawling was conducted with a 400 eastern otter trawl with 4.5-inch stretch mesh between knots in the cod end. Lengths of headrope, footrope, and bridles were 104, 120, and 90 ft, respectively. Seventy-five fm of mudline extended from the bridles to each 850-lb door. Towing speed was 2.5 to 3 knots. Tows were of 3-hr duration in depths of 20 to 44 m, and extended from 6 to 10 km from shore (Figures 77, 78, and 79; Appendix VIII). The total catch was weighed or, for catches over 220 kg, weight was estimated.



FIGURE 77. Location of tows for trawling study during July 1980.

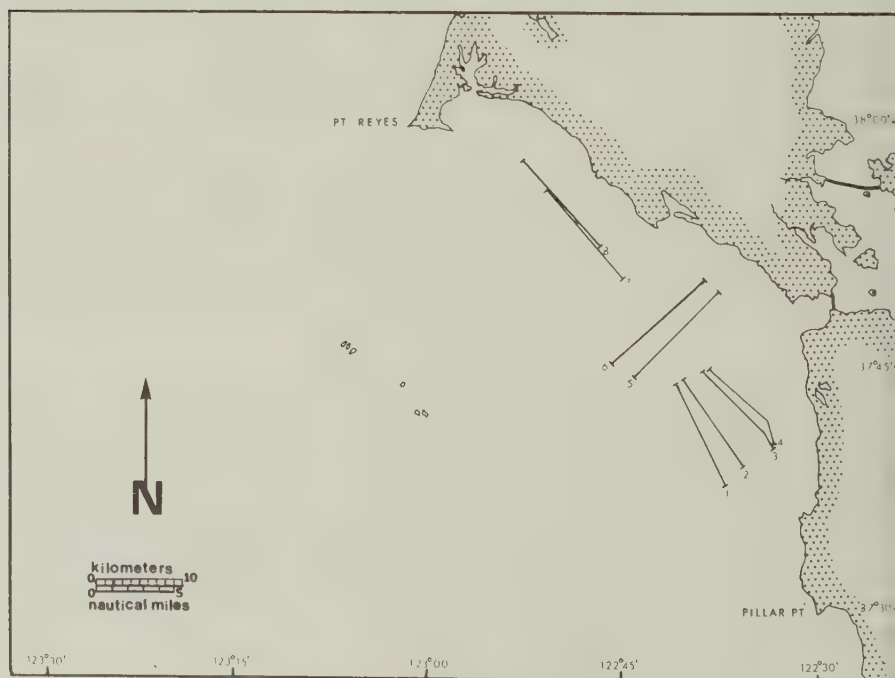


FIGURE 78. Location of tows for trawling study during August 1980.



FIGURE 79. Location of tows for trawling study during September 1980.

With the exception of one tow, all Dungeness crabs were examined to determine size (CW excluding 10th anterolateral spines), sex, and condition of shell (hard, filling, or soft), and whether crabs were alive, dead, or marginal (injured or sluggish). Marginal crabs were placed in a live well with running seawater for 3- to 20-hr observation. One tow was subsampled because of the abundance of crabs.

RESULTS

A total of 3,296 Dungeness crabs, 2,090 males and 1,206 females, was taken in 25 tows (Table 26). Males ranged from 85 to 187 mm CW and females from 78 to 174 mm CW. Number of crabs per tow ranged from 34 to 414. Fish catches ranged from 32 kg to an estimated 4500 kg. Total mortality was 40 males and 24 females, or 1.9% of the total catch. Thirty (75%) of the dead males were of sublegal size (< 159 mm). Nineteen (45%) of the dead males and 14 (58%) of the dead females had soft shells and were crushed by the weight of the catch. An additional 9 (22%) males and 3 (8%) females had filling shells which were fractured or crushed. The remaining hard-shelled casualties either suffered puncture wounds from pews used by the crew to discard fish or sustained broken chelae or legs and (or) had fractured carapaces. Almost all crabs which appeared sluggish with no visible injuries recovered fully after brief immersion in running seawater.

TABLE 26. Fish and Crab Catch by Trawl, July–September 1980.

Date	Tow no.	Fish catch (kg) *	No. male crabs	No. female crabs	Sum	No. dead males	No. dead females	Sum
JUL	9	455	98	109	207	0	3	3
	9	185	19	17	36	0	0	0
	3	4,545	31	51	82	7	6	13
	6	2,275	36	49	85	3	0	3
	5	135	44	60	104	0	0	0
	6	130	18	26	44	0	0	0
	7	340	37	63	100	1	0	1
	8	455	16	41	57	1	1	2
	9	1,365	15	28	43	0	1	1
	10	1,590	22	41	63	1	1	2
	Total	11,475	336	485	821	13	12	25
AUG	3	80	58	25	83	2	2	4
	5	220	107	44	151	2	0	2
	7	30	85	23	108	0	0	0
	7	70	136	37	173	3	0	3
	5	455	52	11	63	0	0	0
	3	170	47	76	123	2	1	3
	6	95	19	19	38	1	0	1
	6	50	16	18	34	0	0	0
	Total	1,170	520	253	773	10	3	13
SEP	7	130	33	20	53	1	0	1
	7	680	278	30	308	1	0	1
	9	455	222	68	290	3	2	5
	9	340	345	69	414	8	0	8
	8	455	94	82	176	0	0	0
	8	455	115	75	190	2	0	2
	10	500	147	124	271	2	7	9
	Total	3,015	1,234	468	1,702	17	9	26
Grand Total		15,660	2,090	1,206	3,296	40	24	64

* All catches greater than 220 kg were estimated

Percentages of total catch of hard, filling, and soft-shelled males killed from trawling operations during the study were 0.9, 1.8, and 20.2%, respectively. The relatively low mortality for soft-shelled crabs may be explained by the following: (i) adult crabs are completely vulnerable for only 1 or 2 hr after molting; after this time the crab becomes mobile and if caught may work itself to the front of the net and escape being crushed; and (ii) fish catches in general were relatively low with only 4 of 25 catches exceeding 1,000 kg. The single heaviest load (4500 kg) accounted for 52% of the total observed mortality during the July study; mortality for that tow was 15.9%. Total mortality was 0.53 crabs per trawling hr for all male crabs and 0.12 crabs per trawling hr for legal-sized males.

DISCUSSION

We believe that the results of this study are a conservative reflection of the mortality that adult Dungeness crabs may suffer during summer commercial trawling operations in the Gulf. The crew members were careful in their handling of crabs and this may not represent typical conditions. Although a majority of the mortality we observed resulted from the crushing of soft and filling crabs by weight of the catch, handling may cause a much higher proportion of the mortality during normal operations. The fact that the term "normal operations" may never be defined is the center of a controversy concerning potential crab mortality due to trawling.

Few data exist on Dungeness crab mortality from commercial trawling operations. Observations on a dragboat working in depths of 36 to 146 m off the Washington coast in December 1947 and January 1948 showed relatively low mortality for Dungeness crabs (Collinsworth et al., 1974). Twenty-five of 588 crabs (4.2%) were damaged seriously enough to cause death. Weights of fish catches were not given. During 8 days of trawling on a 58-ft (19-m) trawler off Eureka in 16 to 50 fm (51 to 98 m) during October–November 1979, the total catch of Dungeness crabs was 18,460 in 34 tows (Peter Quentin Brown, Humboldt State Univ., Arcata Calif., unpublished manuscript). Only 74 (0.04%) were females; 94% were legal males. Mortality was estimated at roughly 5%.

From 1975 to 1980, average annual fishing effort in the Gulf of the Farallones from July to September was approximately 460 trawler hours (Tom Jow, Calif. Dep. of Fish and Game, Menlo Park, unpublished data). We were not able to separate this effort accurately into areas of the Gulf. If all of the effort was confined to the more shallow crab molting grounds, our estimate of 0.53 dead crabs per trawling hr would result in the loss of 244 adult crabs from July to September. If we consider the worst case from our study in which 13 crabs died from a 3-hr tow (4.3 crabs per hr), this would result in the loss of 1,978 crabs during the same 3-month period. However, these relatively low estimates should not be used to dismiss the potential impact of a combination of large fish catches and careless handling of recently-molted Dungeness crabs in trawl catches. The majority of the mortality we observed occurred in females and sublegal males. Any significant fishing mortality suffered by these crabs should be avoided if possible, particularly for enhancement of the depressed Dungeness crab fishery in central California.

Chapter 13

DUNGENESS CRAB ENVIRONMENT PROJECT STUDIES: OBJECTIVES AND APPROACH

by

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INTRODUCTION

The Dungeness Crab Environment Project was established to investigate factors in the environment which could be related to the long-term decline in central California crab landings (Figure 10).

The Dungeness crab, *Cancer magister*, ranges from Amchitka Island, Alaska to the vicinity of Pt. Conception, California. The southernmost fisheries for Dungeness crabs occur in central California in San Francisco, Monterey, and Morro Bay areas (Figure 18). Thus, crab fisheries in central California are near the southern edge of the crab's range where fluctuating environmental conditions, at times, could be expected to approach or exceed tolerable limits at various stages in the crab's life cycle. In addition, the human population along the coast has increased substantially over the last few decades, thereby increasing the potential for degradation of the nearshore environment in estuaries, bays, and the ocean from pollution, land fill, alteration of stream flows, etc.

There is, therefore, the strong possibility that natural and (or) man-caused changes in the environment could have caused or contributed to the long-term decline in central California crab landings as well as other fluctuations in landings along the coast.

Dungeness crab landings in Washington, Oregon, and northern California have shown similar trends for many years (Figure 80). Landings at central California ports also have shown trends somewhat similar to each other including a long-term decline which began about 1960-61 (Figure 81), although, the magnitudes of landings at Monterey and Morro Bay-Avila generally have been much lower than in San Francisco and more northerly areas. Fishing effort is also more variable in the two southernmost areas where landings probably do not reflect crab population trends as well as they do at San Francisco and more northern areas.

Nevertheless, the widespread trends in landings suggest that large-scale phenomena may be responsible for the fluctuations, although local factors may also be important, particularly in areas where crabs may already be stressed from extreme natural conditions.

The objective of the Dungeness Crab Environment Project was to determine whether any natural and (or) man-caused changes in the crab's environment could have caused or contributed to the long-term decline of the crab fishery in central California and other fluctuations in landings along the coast.

Our initial approach was to review the literature, consult various experts in oceanography and pollution, and obtain certain baseline data to provide a foundation for the various investigations.

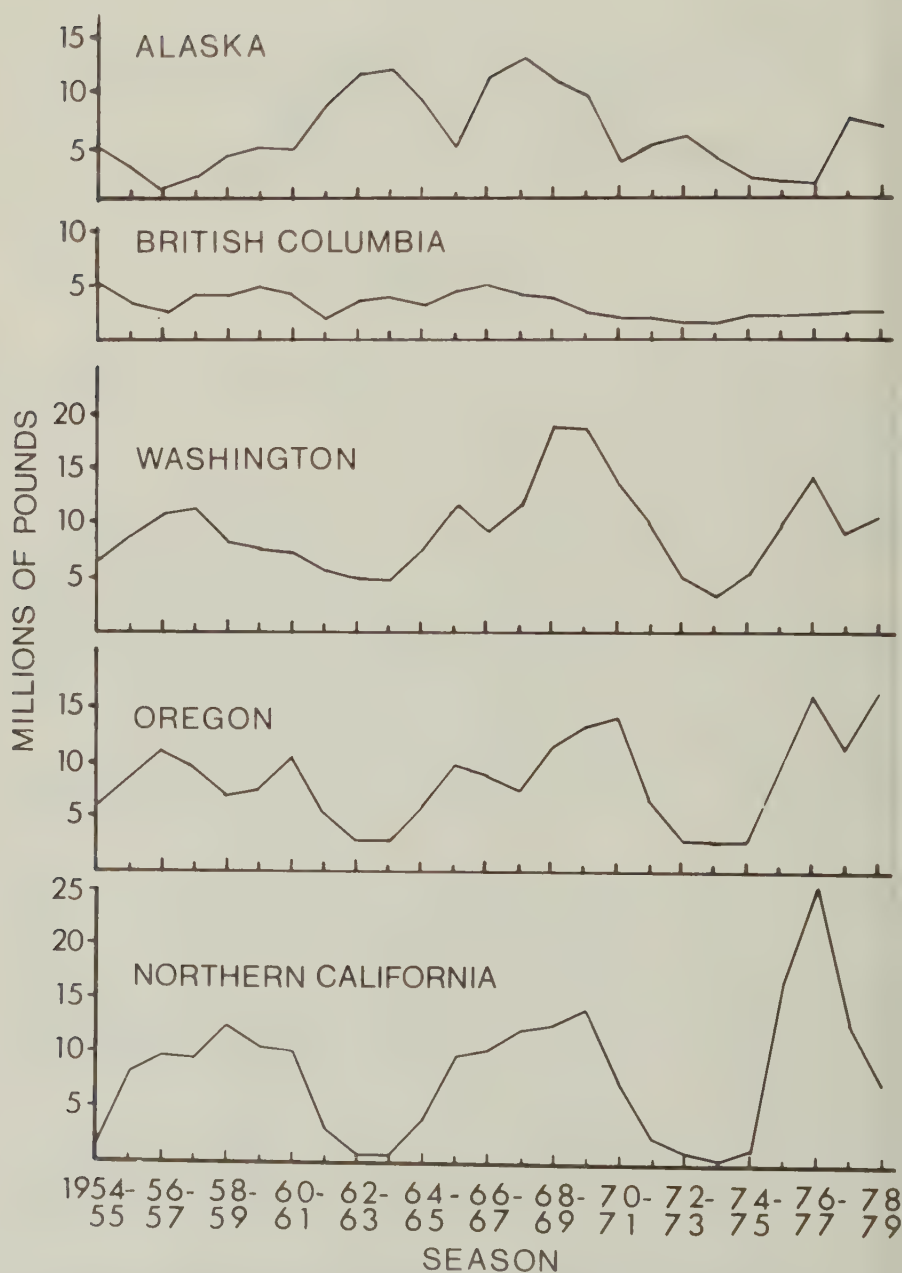


FIGURE 80. Dungeness crab commercial fishery landings by season from Alaska to northern California with the exception that Alaska and British Columbia seasons are calendar years, i.e., 1954-55 = 1955.

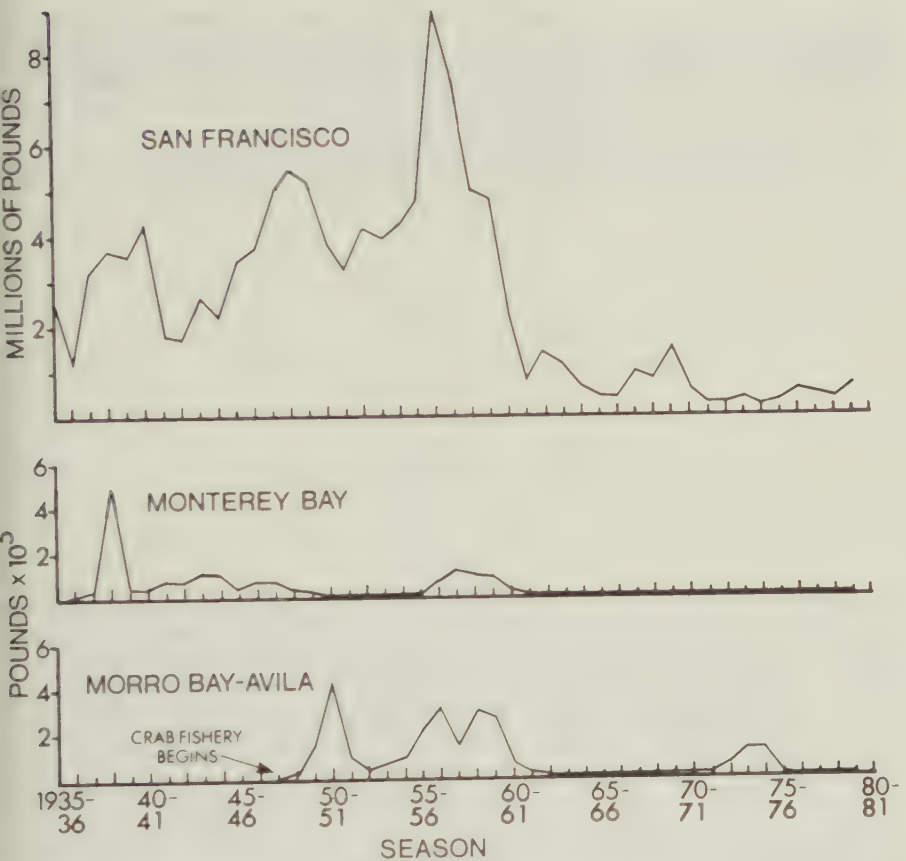


FIGURE 81. Dungeness crab commercial fishery landings by season in central California from San Francisco to Avila. Note expanded scale for Monterey Bay and Morro Bay-Avila.

Historical oceanographic conditions and their relationships to crab landings and crab life history were analyzed and laboratory studies on crab fecundity and relationships of seawater temperature to crab productivity were conducted. Studies on relationships between pollution and crabs were conducted on chlorine-treated domestic sewage, potentially toxic elements, pesticides and PCB's, and hydrocarbons including those of petroleum origin.

Where necessary, cooperative agreements and contracts were established with agencies where appropriate expertise and facilities were available to conduct special studies. These agencies included the Department of Fish and Game (DFG) Water Pollution Control Laboratory at Nimbus; University of California Berkeley's Sanitary Engineering Research¹ and Naval Biosciences Laboratories at Richmond and Oakland; Moss Landing Marine Laboratories; and California Department of Food and Agriculture, Sacramento. The National Marine Fisheries Service, Pacific Environmental Group, Monterey, provided extensive consulta-

¹ Current name: Sanitary Engineering and Environmental Health Research Laboratory.

tion and much of the oceanographic data. DFG Marine Culture and Marine Bioassay² Laboratories provided space and equipment for laboratory experiments and the Biometrics Unit at Menlo Park provided extensive assistance with statistical analyses. The Dungeness Crab Critical Stage Project assisted with collections of samples for several of our studies.

The following seven chapters describe in detail the methods, results, and conclusions of Dungeness Crab Environment Project studies.

² Current name: Marine Pollution Studies Laboratory.

Chapter 14

VARIATIONS IN OCEAN CLIMATE AND THE DUNGENESS CRAB FISHERY IN CALIFORNIA

by

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INTRODUCTION

Variations in the ocean climate are known to affect distribution and abundance of marine organisms and are considered by many to be a possible cause of fluctuations in fishery landings of Dungeness crabs, *Cancer magister*. Historical Dungeness crab landings show similar trends over widespread areas (Figures 80 and 81) which suggest the possibility of relationships to large-scale climatic fluctuations. Of immediate interest to the crab fishery in California is the substantial decline in landings in central California since the 1960–61 season as well as wide-ranging fluctuations in landings in northern California (Figure 10).

In commercial Dungeness crab fisheries, only males 159 mm or larger in carapace width (excluding the 10th anterolateral spines) may be taken legally. In the fishery off central California, the majority of crabs apparently reach legal size at about 3 years of age, although some as young as 2 years and as old as 4 years (or older) occur in the fishery. Off northern California, the commercial catch consists primarily of 4-year-old crabs, but also includes some crabs 3 and 5 years old. Most available legal males are taken in these fisheries each year and commercial landings are considered to be representative of the abundance of exploitable crabs.

No accurate method of aging Dungeness crabs or separating year classes has been developed. Thus, crab landings are the best available index of year classes and spawning biomass. However, because there may be several year classes present in the landings each year, the use of landings as an index of year class abundance is probably an over-simplification.

To ascertain the effect of oceanographic fluctuations on a specific fishery is a rather complex problem. First of all, various oceanographic conditions may affect organisms at different stages in their life cycles. Secondly, annual fishery landings are usually a composite of several year classes, each of which was subjected to different oceanographic influences at their corresponding stages of development.

For analyzing relationships between the oceanographic climate and fluctuations in crab abundance, investigators are limited to those oceanographic param-

eters that are historically observed and recorded. Some of these analyses have been attempted. Winnor (1966) found a multiple correlation ($r=0.76$) between Dungeness crab landings in the San Francisco area and a 4-year lag in January-April sea level, sea surface temperature, and a wind index. Winnor's best partial correlation was with temperature ($r=-0.63$). The sea level record contains a long-term rising trend attributed to glacial melt (Hicks 1978) that was not removed prior to analysis and which may account for some of the multiple correlation.

A positive relationship was suggested between upwelling and Dungeness crab landings in Washington, Oregon, and northern California (Peterson 1973), but at rather short lag-times. The lag-times were $\frac{1}{2}$ year in Washington and $1\frac{1}{2}$ years in Oregon and northern California. Peterson hypothesized that a relationship exists between molting times of crabs and energy flow from the pelagic environment to the benthos. He suggested that later molting by Washington crabs could allow them to be in better pre-molt condition from increased food supplies associated with greater upwelling in the same year.

Botsford and Wickham (1975) using the same data as Peterson, but different statistical techniques, also found a correlation at short lag-times, but with a shorter lag-time in northern California than in Washington and Oregon. Based on statistical modeling, Botsford and Wickham (1978) suggested that the apparent cyclic nature of the crab catch was more likely due to biotic, density-dependent factors such as competition between adults and juveniles.

More recently, McElvey et al. (1980) and McElvey and Hankin (1981), on the basis of statistical modeling, suggested that an egg-larval feedback mechanism dependent upon parent stock density could explain the apparent cycles in northern California crab landings.

These efforts indicate that statistical analyses of historical crab landings, life cycle phenomena, and oceanographic data may suggest relationships between crab abundance and environmental fluctuations which, in turn, may lead to the elucidation of causal effects. Such analyses also suggest field and laboratory studies which may lead to a better understanding of these relationships.

Determining the part that environmental factors may have played in the long-term decline in the central California crab fishery is the underlying motivation in our investigation. We used a variety of statistical techniques to examine these relationships.

OCEAN CLIMATE OFF CALIFORNIA

The ocean climate off central California varies seasonally and is marked by three distinct periods (Skogsberg 1936; Bolin and Abbott 1963). The Davidson Current period, occurring during November through February, is characterized by weak northerly winds, strong winter storm events, inshore northward current flow, and onshore transport of surface water. The upwelling period, occurring from March through August, is characterized by strong northwest winds, southward current flow, offshore transport of surface water, and upwelling of cold nutrient-rich water. The oceanic period, occurring during September and October, is a period of relative calm between the northerly winds of the upwelling period and the southerly winds of winter.

The annual variations can be described in more detail as follows. In late fall and early winter of most years northerly winds are weak and variable, and the nearshore Davidson Current flows northward along the central California coast

This current is reinforced during winter by intermittent periods of southerly winds. The general north northwest-south southeast trend of the coastline and the movement of surface water to the right of the wind due to the Ekman effect cause onshore transport of surface waters and piling up of water against the coast. Minimal winter solar radiation and strong vertical mixing of surface waters by winter storms decrease coastal sea surface temperature (SST) from the autumn peak. While SST declines during the Davidson Current period, nearshore temperatures at 50- to 100-m depths slowly increase due to advection of warm water from the south; temperature at 50-m depth, for example, reaches a maximum during December and January. Due to considerable vertical mixing there is very little vertical temperature gradient during this period. The end of the Davidson Current period is difficult to pinpoint, but is usually evident about March when the atmospheric North Pacific high pressure cell intensifies and northwest winds become frequent along the coast. These conditions cause offshore transport of surface water and, in the nearshore region, some of this water is replaced by cold, nutrient-rich subsurface water upwelled from the upper hundred meters or so and strong vertical temperature gradients form. Upwelling is strongest when northerly winds are strongest and, near San Francisco, usually reaches a maximum in June or July (Bakun 1975). By August, northerly winds begin to slacken and the strong solar radiation of summer results in a steady rise in SST that usually continues through September. A period of calmer winds begins in September or October that Skogsberg (1936) called the oceanic period. With a slackening of windstress, the cool, upwelled water begins to sink and is replaced by warmer surface water from offshore. Coastal SST rises to the highest seasonal values and vertical temperature gradients are deeper.

Although the annual cycle reoccurs each year, there are also longer-term fluctuations in the ocean climate. One of the best-documented fluctuations in the ocean climate off California began in the fall of 1957 when much higher than normal water temperatures and sea levels (as recorded at coastal tide gages) became evident. This change in ocean climate was well documented in a symposium on "The Changing Pacific Ocean in 1957 and 1958" (Sette and Isaacs 1960). Huang (1972) analyzed sea level variations off southern California and their contributing factors along the coast and concluded that this change in ocean climate began in 1957 and signalled a regime that persisted for at least a decade. Namias and Huang (1972) showed that, by far, the greatest cause of the high sea levels was a thermal effect. The surface layer of water off southern California averaged 1 C higher during the decade 1958-1967 than during the earlier one (1948-1957). This warming was associated with weaker northwesterly winds and anomalously stronger southwest wind components in the later decade which, in turn, resulted in more eastward oceanic flow from the subtropics and less southward flow from the California Current system. The thermal effect was most evident during winter months. These effects suggest that the Davidson Current was also more intense during the later decade.

It is of interest that the decline in the Dungeness crab fishery off central California (Figure 10) began in the 1960-61 season, 3 years after the onset of this climatic change in the ocean.

CORRELATIONS AMONG ENVIRONMENTAL DATA

Historical time series of monthly mean values of a variety of environmental parameters were obtained from the NMFS Pacific Environmental Group, Monte-

rey, California. Five parameters were chosen which reflect major fluctuations of ocean conditions off central California that may be related to survival of Dungeness crabs, and for which reasonably complete historical records are available (Figure 82).

The first parameter is sea level which is the monthly mean of hourly tide heights recorded at the San Francisco tide gage. Sea level would not affect crabs directly but, instead, sea level measurements represent an integration of several coastal oceanographic processes and fluctuate in response to them (Chelton 1980; Bretschneider 1980). The sea level record at San Francisco began in 1856 and exhibits a secular, rising trend. This trend, apparent in many sea level records, is attributed to glacial melt occurring since the last ice age and contributes about 1.3 mm per year to the San Francisco record (Hicks 1978). We removed this secular trend by subtracting a least squares fitted line from the data. This detrended sea level record was not adjusted for the inverse barometer effect of atmospheric pressure.

Two series of data were used to represent fluctuations of water temperature. The first is monthly means of SST observations made by passing merchant ships in a 1° square of longitude and latitude off San Francisco. The second series is monthly means of daily SST observations at the San Francisco tide gage station. These shore station temperature data are probably not as representative of coastal water temperatures as are the merchant ship data due to local distorting effects in nearshore shallow water and effects of the San Francisco Bay estuary.

The fourth environmental parameter is monthly mean atmospheric pressure as observed at San Francisco International Airport. This parameter is an indicator of large-scale variations of winds and atmospheric circulation.

The final series is an index of upwelling at 39° N, 125° W (Bakun 1973). This parameter represents the onshore-offshore transport of surface water by winds near the coast due to the Ekman effect.

As a first step in analyzing these data, we used quarterly means of each series to make 20 environmental variables (five parameters $\times$ four quarters) and ran correlations among them. Because each series had different time spans of historical data available, and some had gaps in the data, we restricted the correlations to selected years of available data.

Several of the variables were significantly correlated with each other but sea level was most consistently correlated significantly with all the rest (Table 27). Sea level was significantly correlated with all four of the other parameters in the first and fourth quarters. Sea level was significantly correlated with merchant ship SST during all four quarters; the highest of these correlations (0.76) was obtained in the fourth quarter (Table 27). Also of interest was a slightly higher coefficient ($r = 0.77$) found between third quarter sea level and fourth quarter SST. A possible explanation for this relationship is that sea level responds rapidly to changes in ocean circulation, whereas SST may take several months to exhibit maximum response to a circulation change.

Sea level was correlated with shore station SST only in the first and fourth quarters, but not as strongly as merchant ship SST, suggesting that the shore station SST is a less effective monitor of oceanographic changes off San Francisco.

Fairly strong correlations were found between sea level and atmospheric pressure and upwelling during the winter months (fourth and first quarters). The

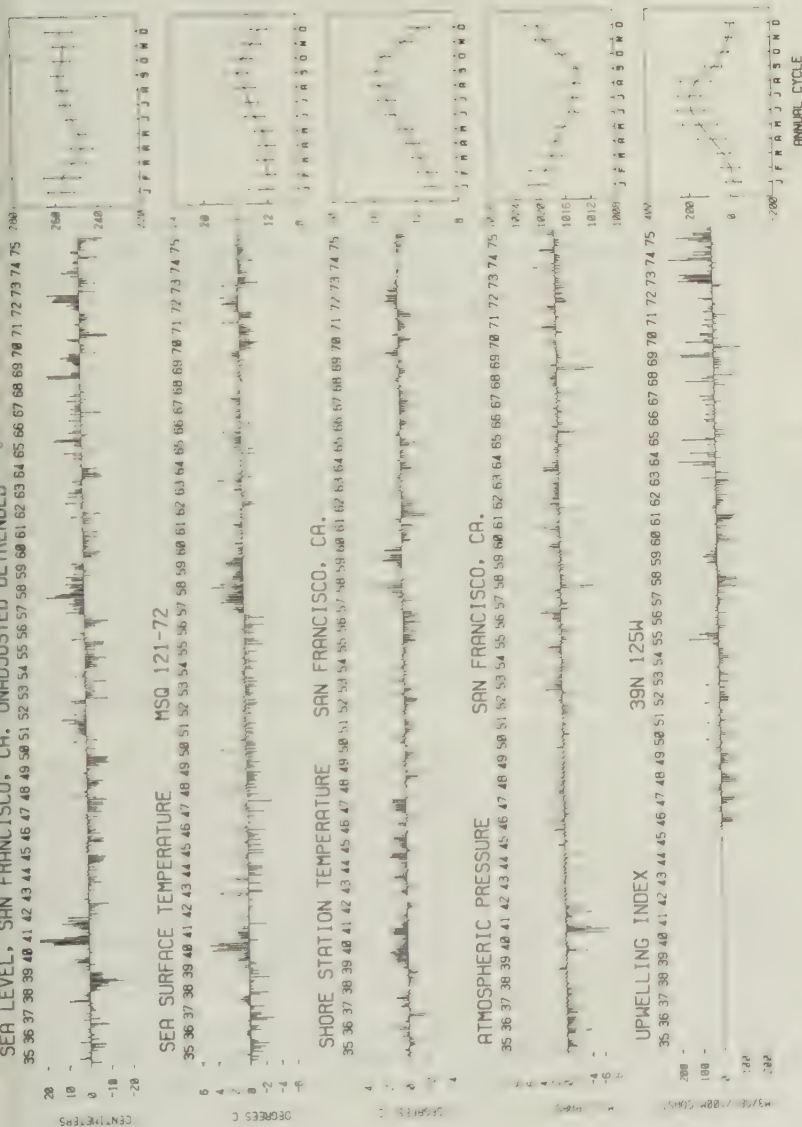


FIGURE 82. Monthly anomalies of environmental data series from 1935 through 1975.

Table 27. Correlation Coefficients of Sea Level Versus other Environmental Parameters by Quarter

<i>Quarter</i>	<i>Sea surface temperature</i>	<i>Shore station temperature</i>	<i>Atmospheric pressure</i>	<i>Upwelling index</i>
First (Jan-Mar)	0.56 *	0.45 *	-0.78 *	-0.59 *
Second (Apr-Jun)	0.54 *	0.23	-0.60 *	-0.19
Third (Jul-Sep)	0.67 *	0.02	-0.18	-0.01
Fourth (Oct-Dec)	0.76 *	0.36 †	-0.47 *	-0.34 †

* Significance: $P < 0.01$ † Significance: $P \leq 0.05$

correlations with atmospheric pressure probably reflect the inverse barometer effect of pressure on sea level which was not corrected for in this sea level series. The significant negative correlations of sea level with upwelling index reflect winter onshore transport and downwelling.

CORRELATION OF LANDINGS WITH ENVIRONMENTAL DATA

Fluctuations in environmental conditions would be expected to have their greatest effects upon the most sensitive crab life stages such as eggs, larvae, or juvenile stages. The impact on crab abundance would become obvious in crab landings when a particular year class of crabs matured to catchable size, which occurs up to several years after the environmental change. To analyze for this time-lag effect, we lagged each year of San Francisco area crab landings during 1945 to 1978 from 0 to 6 years with each oceanographic data series to construct seven time-lagged landings variables per series. Ricker (1975) suggested that influences of environmental parameters on a particular fishery are multiplicative rather than additive, hence we also used the natural log of the various time-lagged landings in most of our analyses.

Correlation coefficients were computed among landings and environmental variables to produce a correlation matrix of the seven landing variables and the 20 environmental variables (Table 28). We looked for trends and clusterings of significant correlations in this matrix which might indicate relationships between variables and landings. We recognize that environmental and landings data series both show some year to year persistence and thus each data point in a series may not be completely independent of adjacent points. However, we used a correlation analysis program which assumes complete independence of data points and computes significance levels based on this assumption.

Most of the correlations between crab landings and environmental variables produced rather low correlation coefficients (Table 28). However, there were several coefficients of 0.3 to 0.5 magnitude that were statistically significant, and which may suggest possible causal relationships. Using the log of landings did not improve these correlations.

Sea level was primarily negatively correlated with landings. Third quarter sea level at 2- and 3-year lags and fourth quarter sea level at 1-, 2-, and 3-year lags show the highest correlations for this parameter. This suggests that sea level conditions during oceanic and Davidson Current periods may be related to abundance of crabs.

TABLE 28. Correlation Coefficients of Environmental Parameters by Quarter versus Crab Landings at Lags of 0 to 6 Years.

Parameter	Quarter*	Lag time in years						
		0	1	2	3	4	5	6
Sea level	1	-0.11	-0.25	-0.23	-0.27†	-0.18	-0.11	-0.13
	2	0.20	0.05	0.02	0.12	-0.02	0.14	0.05
	3	-0.13	-0.29*	-0.39†	-0.41†	-0.28†	-0.17	-0.22
	4	0.31*	-0.44‡	-0.43‡	-0.42‡	-0.25	-0.16	-0.13
Sea surface temperature	1	0.03	0.00	0.10	-0.20	-0.25	-0.30	-0.37†
	2	0.33†	0.18	0.04	-0.18	-0.17	-0.20	-0.15
	3	0.06	-0.11	-0.18	-0.27	-0.28	-0.26	-0.32
	4	0.01	-0.19	-0.23	-0.35†	-0.33†	-0.21	-0.20
Shore station temperature	1	-0.12	-0.18	-0.06	-0.04	0.08	0.08	0.06
	2	0.36†	0.32*	0.27†	0.19	0.17	0.11	0.15
	3	0.05	0.02	0.00	0.13	0.10	0.11	0.27†
	4	0.06	0.04	0.11	0.19	0.19	0.24	0.32†
Atmospheric pressure	1	-0.06	-0.02	-0.04	0.06	-0.05	-0.11	-0.11
	2	-0.15	0.08	-0.16	-0.09	-0.13	-0.28†	-0.17
	3	0.09	-0.04	-0.13	-0.12	-0.18	-0.11	-0.02
	4	0.18	0.17	0.13	-0.03	-0.18	0.23	-0.27†
Upwelling index	1	-0.01	-0.01	0.13	0.31†	0.36†	0.37†	0.27
	2	-0.56‡	-0.47‡	-0.45‡	-0.39†	-0.37†	-0.39†	-0.40†
	3	-0.35*	-0.29	-0.34†	-0.37†	-0.34†	-0.33†	-0.37†
	4	-0.16	-0.08	-0.21	-0.15	-0.23	-0.20	-0.15

* Quarters are: 1) Jan-Mar; 2) Apr-Jun; 3) Jul-Sep; 4) Oct-Dec

† Significance: $P < 0.05$ ‡ Significance: $P < 0.01$

Merchant ship sea surface temperatures show significant values in the second quarter at a 0-year lag and first quarter at a 6-year lag. These results appear fortuitous as it would be difficult to explain any relationships at these lag times because most crabs are caught each year early in the first quarter and very few legal crabs reach 5 or 6 years of age. Other correlations of interest occur in the fourth quarter at 3- and 4-year lags. Sea surface temperature is highly correlated with sea level and the correlations of landings with temperature suggest a relationship to ocean conditions during the Davidson Current period similar to sea level.

Shore station temperatures were mostly poorly correlated with landings but show the highest values in the second quarter at 0-, 1-, and 2-year lags and fourth quarter at a 6-year lag.

Atmospheric pressure, overall, showed the lowest correlations of the environmental parameters used.

The upwelling index was positively correlated with landings in the first quarter at 2- through 6-year lags, and was negatively correlated at all other quarters. The second and third quarters had the highest negative correlations at all lag times, which may be due to a rising trend in the upwelling index (Figure 82) and the decreasing trend of landings. These correlations may suggest, however, that

strong upwelling, or related processes, in spring and summer are detrimental to crab abundance.

Factor analysis was performed on the 20 environmental variables to select for further analyses a smaller group of these variables which accounts for a major proportion of variations in the original data series. The method of principal factoring with iteration and orthogonal varimax rotation (Nie et al. 1975) was used for this analysis. The principal factoring procedure stopped after six iterations when communalities exceeded one. Eight principal factors resulted. The factor (loading) matrix was displayed after varimax rotation with Kaiser normalization. By examining this matrix and retaining only those variables with factor loadings greater than 0.6 and discarding variables within each principal factor that were highly correlated, 11 environmental variables, which account for a major proportion of the variation among the series, were selected for further analyses. The variables selected were first, second, and third quarter sea level; fourth quarter sea surface temperature; first, second, and fourth quarter shore station temperature; second and third quarter atmospheric pressure; and third and fourth quarter upwelling.

Since crab landings off San Francisco declined after the onset of a change in the oceanographic climate in 1957 and landings have still not recovered, we applied Rao's stepwise discriminant analysis to the resultant variables to determine whether there was any significant function that would discriminate well between the pre-1957 and post-1956 environmental conditions. Stepwise discriminant analysis of the 11 variables stopped after seven steps when criteria of F to enter and F to remove, both equalled 1.0 and minimum tolerance equalled 0.001. A discriminant function made up of seven variables was obtained. Standardized canonical discriminant function coefficients were:

<i>Variables</i>	<i>Coefficient</i>
1st quarter sea level	-0.97
2nd quarter sea level.....	1.10
4th quarter sea surface temperature	-2.52
4th quarter shore station temperature	0.61
2nd quarter atmospheric pressure.....	-1.00
3rd quarter upwelling	-0.95
4th quarter upwelling	-0.80

Discriminant scores were calculated for each year as follows: Discriminant score = Σ (standardized variable value $\times$ discriminant coefficient). Each standardized variable had a mean of zero and variance of one.

The discriminant scores show a significant difference between the pre-1957 and post-1956 years (Figure 83). The group mean for the pre-period was 2.89 and for the post-period, it was -1.65. Of the seven variables, fourth quarter sea surface temperature stands out as a major contributor to the discriminant function for the two periods. High mean temperature for this variable tends to be representative of post-1956 years.

One-way analysis of variance was performed to test for differences between the pre-1957 and post-1956 periods for these seven variables. Post-1956 fourth quarter mean sea surface temperature and third quarter mean upwelling were both significantly higher than during the pre-1957 period ($P = 0.01$ and 0.02 , respectively). None of the other variables showed significant differences ($P > 0.1$) in this test.

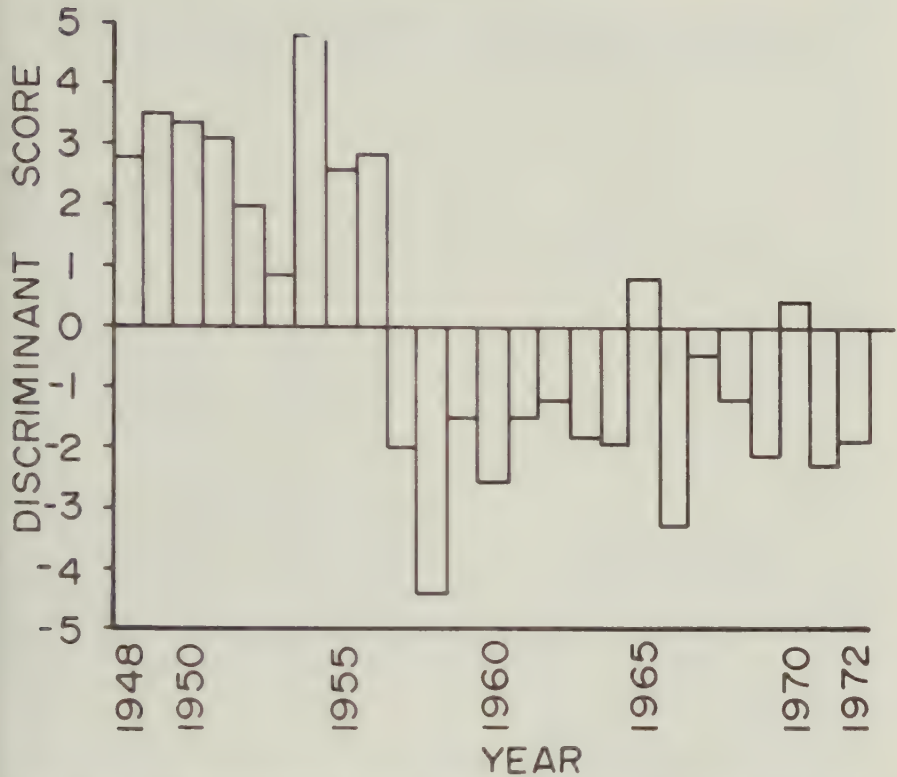


FIGURE 83. Discriminant scores for years 1948–1972 using environmental variables selected by stepwise discriminant analysis.

Canonical correlation was used to determine if there were any linear composite functions of these resulting variables which would correlate well with a composite of the logs of landings. No significant canonical correlation functions were found.

To test further for relationships between environmental variables and crab landings, multiple stepwise regressions were run with the seven variables from the discriminant analysis on 2-, 3-, and 4-year lags of log of landings. The minimum F to enter and maximum F to remove a variable both equalled 1.0, and the minimum tolerance equalled 0.001.

Coefficients of determination (r^2) from these multiple regressions were 0.66, 0.65, and 0.69 for 2-, 3-, and 4-year lags, respectively (Table 29). Fourth quarter sea surface temperature and second quarter atmospheric pressure contributed most to the r^2 change at all lags. However, second quarter atmospheric pressure contributed the most at the 2-year lag while fourth quarter sea surface temperature contributed the most at 3- and 4-year lags.

This analysis suggests that there is a relationship between ocean climate and the Dungeness crab fishery in central California. Furthermore, it points to fourth quarter sea surface temperature and second quarter atmospheric pressure as indicators of ocean conditions which may have important effects on crab abundance.

Table 29. Summary of Stepwise Multiple Regressions of 2-, 3-, and 4-Year Lags of Log of Landings on Variables Selected in Discriminate Analysis*.

Step	Variable		Multiple <i>r</i>	<i>r</i> ²	<i>r</i> ² change	Overall <i>F</i>	Signi- ficance
	Entered	Removed					
(2-year lag)							
1	ATP-2		0.53	0.28	0.28	7.37	0.014
2	SST-4		0.70	0.49	0.21	8.77	0.002
3	UPW-3		0.79	0.62	0.13	9.36	0.001
4	SEL-2		0.81	0.66	0.03	7.63	0.001
(3-year lag)							
1	ATP-2		0.44	0.19	0.19	4.55	0.046
2	SST-4		0.66	0.44	0.25	7.11	0.005
3	UPW-3		0.73	0.53	0.09	6.38	0.004
4	UPW-4		0.76	0.58	0.05	5.60	0.005
5	SEL-1		0.80	0.65	0.06	5.51	0.004
(4-year lag)							
1	ATP-2		0.39	0.15	0.15	3.46	0.078
2	SST-4		0.61	0.37	0.22	5.28	0.016
3	UPW-3		0.68	0.47	0.10	4.94	0.012
4	UPW-4		0.74	0.55	0.09	4.97	0.008
5	SEL-1		0.79	0.62	0.66	4.90	0.007
6	SEL-2		0.84	0.71	0.09	5.72	0.003
7		ATP-2	0.83	0.69	-0.02	6.77	0.002

* Variables selected in discriminant analysis.

- 1st Qtr. Sea level - SEL-1
- 2nd Qtr. Sea level - SEL-2
- 4th Qtr. Sea surface temperature - SST-4
- 4th Qtr. Shore Station Temperature - SHT-1
- 2nd Qtr. Atmospheric pressure - ATP-2
- 3rd Qtr. Upwelling - UPW-3
- 4th Qtr. Upwelling - UPW-4

DISCUSSION

Our analyses of the ocean climate substantiate earlier evidence by Huang (1972), Namias and Huang (1972), and others of a significant change in the ocean climate which began in 1957. Our analyses further demonstrate that this change continued into the 1970's.

Huang (1972) concluded that southward flow of the California Current weakened during the decade after 1957 relative to the prior decade and that northward flow of the nearshore countercurrent (Davidson Current) may have increased. These changes resulted in the advection of more warm, high salinity tropic and subtropic water, and less cold, low salinity subarctic water into the California Current region. Both water temperature and sea level are indicators of this major change in the ocean climate.

Correlations between ocean climatic variables and crab landings do not necessarily reflect cause and effect relationships. Such correlations must be explainable in terms of biological and oceanographic phenomena and where possible should be supported by laboratory and field studies to lend credibility to them. Significant correlations suggest possible relationships and can be used to provide input to design further investigations and to plan resource management strategies.

The correlations we obtained between landings and oceanographic variables at various lag times suggest the possibility of effects of ocean climate on reproduction and early life stages of Dungeness crabs. Third and fourth quarter sea level and sea surface temperatures were correlated well with each other. The correlations between these variables and crab landings at 2-, 3-, and 4-year lags suggest possible effects on early crab life stages such as ovary development, spawning, egg development and hatching success, and larval survival.

Examinations of female crabs from central and northern California during 1976–1979 showed differences in ovary development. Smaller ovaries, on the average, were observed in crabs in central California (Wild, Chapter 15). Physiological responses to environmental conditions, such as warmer ocean temperatures in the southern portion of the crab's range, could explain these differences.

In central California, Dungeness crabs spawn and brood their eggs primarily during October through December. In the laboratory, survival of Dungeness crab eggs and hatching success were adversely affected at seawater temperatures which have commonly occurred during October–December off central California during the crab decline (Wild, Chapter 16). Warm fourth quarter SST is the most important discriminator of post-1957 years in our analysis. Due to strong vertical mixing in the nearshore water column during winter (Davidson Current period), SST is a good index of bottom temperatures which the crabs experience during the egg brooding period in central California. Thus, warm ocean temperatures during egg brooding periods since 1957 could have contributed to the decline in landings in central California (Figure 84) by affecting egg survival and hatching success.

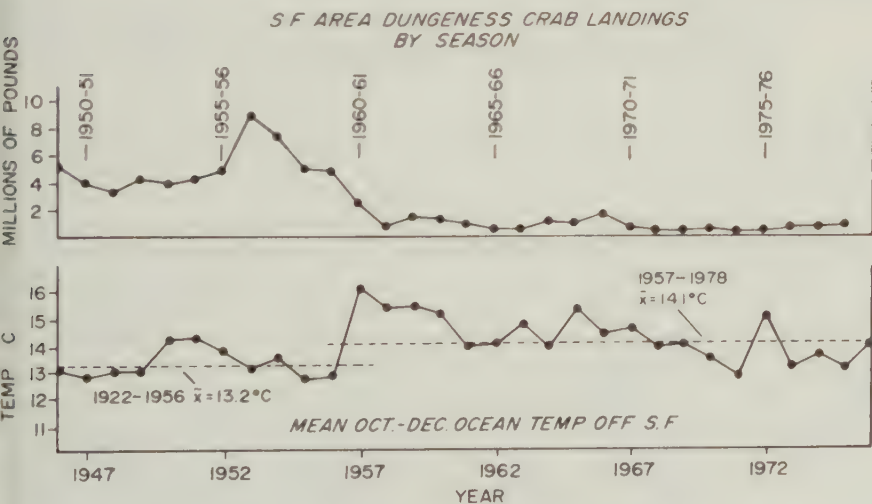


FIGURE 84. Commercial fishery landings of Dungeness crabs in the San Francisco area by season, 1949–50 through 1978–79, and mean Oct.–Dec. ocean temperatures, 1946 through 1975. Landings are shown lagged 3 years relative to temperature.

Furthermore, comparisons between ocean temperatures during the egg brooding period in northern California and crab landings 4 years later suggest relationships between ocean climate, survival of early life stages, and wide-

ranging fluctuations in the crab catch there (Figure 85). It is of interest that the highest crab landings on record in California (1975-76 and 1976-77 seasons; Figure 2) were primarily from a year class that was produced during the lowest November to January (1971-72) ocean temperatures in that area since the 1940's (Figure 85).

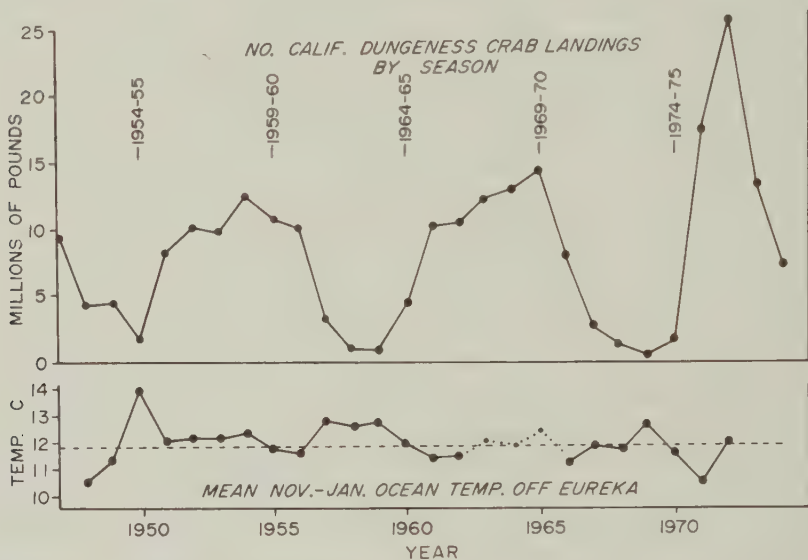


FIGURE 85. Commercial fishery landings of Dungeness crabs in northern California by season, 1951-52 through 1978-79, and mean Nov.-Jan. ocean temperatures, 1948 through 1972. Landings are shown lagged 4 years relative to temperature. (Dotted line is Blunt's Reef temperature substituted for missing data in the merchant ships series.)

In central California, Dungeness crab larvae hatch primarily during December and January in areas from shore to approximately 100-m depths and are planktonic in the upper water layers during larval development. Anomalously warm temperatures and high sea levels during these months are typically associated with a stronger Davidson Current which, in addition to adversely affecting egg survival from a direct thermal effect, also could transport newly-hatched larvae northward from the area of hatching. The significance of such northward transport is as yet unknown and such northward movement of crab larvae has not been documented. There is, however, evidence that planktonic organisms along central California are transported northward during the Davidson Period and southward during the upwelling period (Hatfield, Chapter 8).

The later larval stages are found progressively further offshore except for megalopae, the last larval stage, which are found concentrated nearshore, usually in April or May just after the onset of upwelling (Reilly, Chapter 6). The transport mechanism by which megalopae arrive inshore is, as yet, unknown. The correlation of second quarter atmospheric pressure with crab landings in the stepwise multiple regression (Table 29) may be related to ocean circulation processes which could affect such larval distribution. However, atmospheric pressure was not strongly correlated with landings in the simple regressions (Table 28).

Second quarter upwelling was significantly negatively correlated with landings (Table 28). Strong spring upwelling has occurred more frequently since 1964 (Figure 82) and presumably could prevent many megalopae from arriving in favorable nearshore settling areas.

Megalopae settle to the bottom and metamorphose to the first juvenile crab stage in the nearshore area primarily during April and May in central California. Subsequently, during summer and fall, many early stage juveniles crabs are found in San Francisco and San Pablo Bays in addition to the nursery areas along the open coast (Tasto, Chapter 10). Bay-reared juveniles molt more frequently and thus grow faster than those in the ocean. They migrate back to the ocean about 1 year (about $1\frac{1}{2}$ years of age) after entering the Bay. The full impact of estuarine and ocean conditions on juveniles is not known. Predation and cannibalism may be substantial in this period (Reilly, Chapter 11), particularly during molting when the crabs' exoskeletons are in a soft condition and the crabs are relatively defenseless.

Botsford and Wickham (1978) and Winnor (1966) suggest that density-dependent cannibalism by adults upon juveniles may explain apparent cyclic fluctuations in crab landings. Such fluctuations are particularly evident in landings from northern California to Washington. Our statistical analyses and field and laboratory studies point more strongly to effects of ocean climate on earlier life stages as possible causative factors of the fluctuations in landings. McElvey et al. (1980) and McElvey and Hankin (1981) have concluded that the cycles in northern California landings are too long to be caused by density dependent cannibalism on juveniles. Based on statistical modeling, they suggest that an egg-larval feedback mechanism dependent on stock egg capacity would cause the observed fluctuations.

San Francisco Bay-reared juvenile crabs become sexually mature at about the time they migrate back to the ocean at approximately $1\frac{1}{2}$ years of age. Ocean-reared crabs are probably 2 years or older before sexual maturity is reached. Approximately 11 to 14 molts are required to reach this stage. The adults molt only once each year and growth increments are greater for adult males than for adult females.

The changes in ocean conditions we examined probably have less impact on adult crabs than earlier life stages. However, mortality of adults in the laboratory was progressively greater at temperatures above 10 to 11 C (Wild, Chapter 16) which suggests that the crab's life span may be shorter in the warmer, more southern areas of their range. The positive correlations found by Peterson (1973) and Botsford and Wickham (1975) between upwelling and crab landings at short lag times of $\frac{1}{2}$ to $1\frac{1}{2}$ years in northern California, Oregon, and Washington may suggest effects upon adult crabs such as the food-chain energy-flow hypothesis suggested by Peterson. However, the order of lag times by areas were conflicting in these two studies, and we do not see any evidence of a link to the central California crab fishery decline.

In some recent winters (particularly 1971, 1973, and 1975) water temperatures in central California have reverted to cooler values and thus presumably were more favorable for crab productivity. However, spring and summer upwelling also have been anomalously strong during most years since 1964 (Figure 82) and this could have caused increased offshore transport of larvae and decreased inshore movement of megalopae. Such an effect could have kept

larval survival low even with more favorable conditions for egg survival and hatching. More analyses of such factors are needed to provide a better understanding of the dynamics and relationships involved, particularly of inshore transport mechanisms for megalopae.

In conclusion, the evidence for the major cause of the decline in fishery landings in the San Francisco area points strongly to a major, long-term fluctuation in the ocean climate. Huang (1972) suggested that the California Current regime was shifted northward and eastward in the decade after 1958. Concurrently the southernmost area of major crab abundance shifted northward off northern California and fluctuations in crab landings there also appear to be related to fluctuations in the ocean climatic regime. These conclusions are supported by various statistical analyses and empirical laboratory and field studies.

Chapter 15

COMPARISONS OF OVARY DEVELOPMENT IN DUNGENESS CRABS, *CANCER* *MAGISTER*, IN CENTRAL AND NORTHERN CALIFORNIA

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INTRODUCTION

Dungeness crabs, *Cancer magister*, are extremely fecund animals. Female Dungeness crabs annually spawn egg masses which may contain from one to two million eggs per crab. This high reproductive potential is necessary to maintain crab populations which experience high mortalities from environmental conditions, predation, etc. during their early life stages.

In analyzing possible causes of the long-term decline in the central California crab fishery (Figure 10), it was important to compare crab fecundity in central California to other areas. This study obtained information on relative fecundity by comparing maturity rates and weights of Dungeness crab ovaries in central and northern California.

Dungeness crab ovaries are known to undergo color changes as they mature (Spencer 1932; Waldron 1958). Ovarian size and color changes have been related to histological changes in the blue crab, *Callinectes sapidus* (Hard 1942), and the deep sea red crab, *Geryon quinquedens* (Haefner 1977). Ovarian color changes also were used to describe maturation stages of the calico scallop, *Argopecten gibbus* (Miller et al. 1979).

The crab ovary is a bi-lobed structure with two anterolateral lobes joined by a bridge behind the stomach and two posterior lobes which fuse posteriorly as the ovary matures (Warner 1977). Paired reproductive tracts connect the ovary to a pair of external genital openings on the crab's sixth thoracic sternite. In an immature crab, the ovary consists of thin, many-branched, translucent tubules (Waldron 1958). In a mature Dungeness crab, the developing ovary increases in mass and undergoes color changes from white to pinkish, to light orange, to orange, to red-orange, and to red before the crab spawns, at which time the ovary occupies a major portion of the crab's interior. However, spawned eggs and, therefore, newly spawned egg masses are usually bright orange in color. Female crabs become sexually mature and the ovaries begin to function at an average carapace width of about 100 mm (Weymouth and MacKay 1936; Butler 1960) or, as recent studies indicate, possibly at a somewhat smaller average size in San Francisco Bay (Tasto, Chapter 9).

METHODS AND MATERIALS

Female Dungeness crabs were collected from the ocean in the vicinity of San Francisco (central California) and Eureka (northern California) intermittently

during 1976–1979. Most of the crabs were collected with crab traps or by trawling aboard Department of Fish and Game research and patrol vessels and commercial crab boats. Some ovigerous (berried) crabs were collected intertidally from the sand during December 1977 and 1979 by walking beaches during minus tides. The crabs were frozen as soon as possible after collection and were dissected and examined later in the laboratory. We examined 629 crabs including 304 from the Eureka area and 325 from the Gulf of the Farallones (San Francisco area).

Carapace width (excluding the 10th anterolateral spines) was measured to the nearest millimeter. To facilitate removal of the ovary, a cut was made in the carapace along and just ventral to the anterolateral spines, extending from the crab's mouth to the rear edge of the carapace on both sides. This allowed the top of the carapace to be lifted off exposing the internal organs.

Ovarian tissue was removed with forceps, blotted on a paper towel, weighed to the nearest 0.1 g, and the color recorded. Ovary colors were compared to a Windsor and Newton's Designer's Gouache color chart as follows: light orange—color chart numbers 574 and 586; orange—517 and 521; red-orange—520 and 582; red—506 and 584 (this color chart does not have white). Maturity of the ovaries was evaluated statistically by use of a color code for ovary colors ranging from white to red, numbered from one to five.

Beginning about midway in the study, diameters of developing ova were measured. For these measurements, a sample of ovarian tissue was placed on a microscope slide and examined under a compound microscope fitted with an ocular micrometer. Approximately 10 developing ova per sample were measured. Validity of the color code as an index of maturity was evaluated by regressing mean diameters of developing ova on ovary color. Maturity rates were analyzed statistically by area and compared for differences.

Because of considerable variation in crab widths and ovary weights within and between samples, it was necessary to standardize ovary weights for comparisons. However, crabs often have limbs missing and newly regenerated limbs are smaller than normal, thus crab weights were not usable for calculating standardized ovary weights (percentage of body weight). Therefore, crab volumes were determined for a wide size range of live crabs by over-flow displacement in seawater. A close relationship was found between crab width and crab volume (Figure 86). All crab widths were converted to volumes and standardized ovary weights were calculated as follows:

$$\text{standardized ovary weight} = \frac{\text{ovary weight}}{\text{crab volume}} \times 100.$$

A 13-month scale, based on spawning time which begins about October in California, was used for comparisons of ovary development with time. Crabs collected in October with newly-spawned egg masses were placed in month number 1. October crabs which had not yet spawned were placed in month number 13. No crabs were collected in November and all other crabs were placed in their respective month of collection.

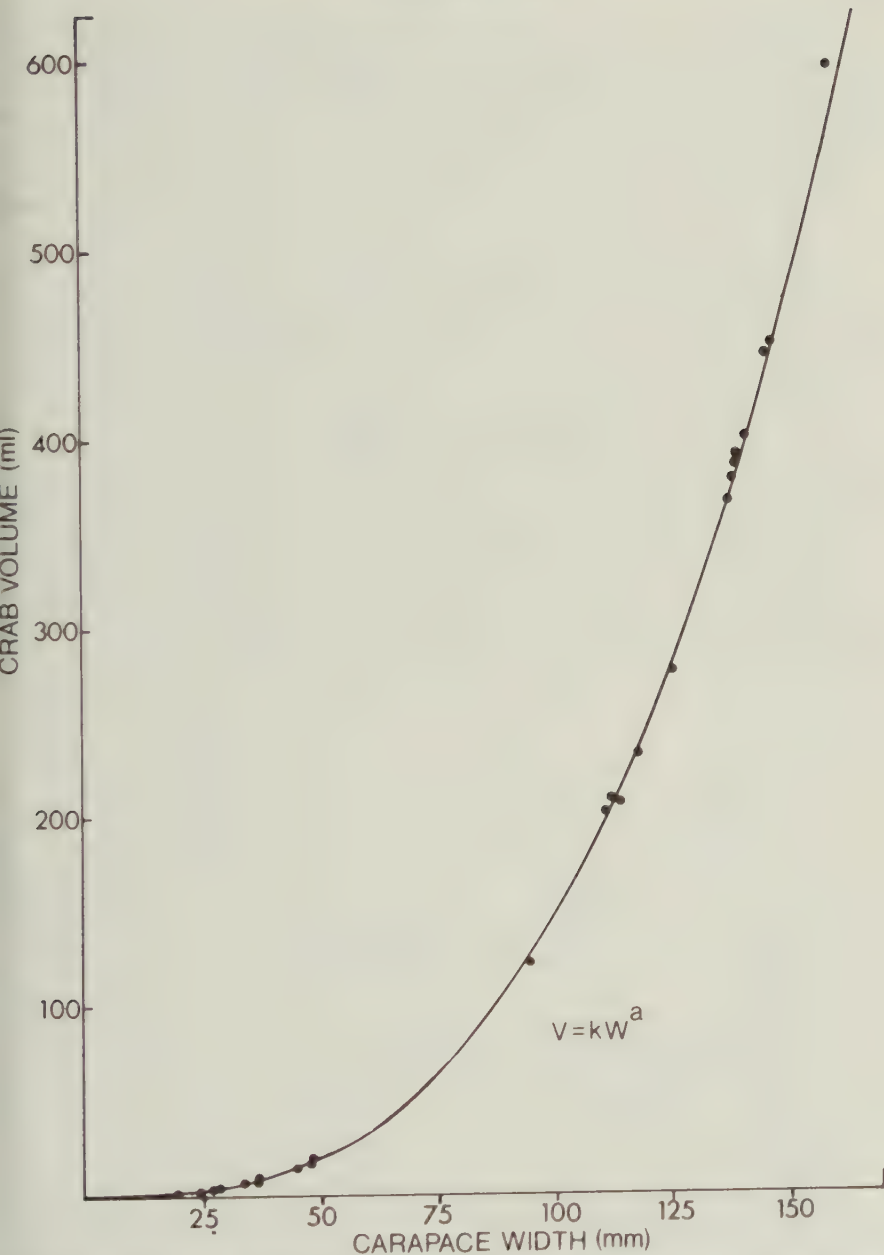


FIGURE 86. Relationship between female Dungeness crab width and volume (V = crab volume; $k = 2.34 \times 10^{-4}$; W = crab width; $a = 2.9$).

RESULTS

Most months of the year were represented in collections of San Francisco and Eureka area crabs from June 1976 to December 1979 (Table 30). Crabs from the San Francisco area ranged from 93 to 172 mm in carapace width and Eureka area crabs ranged from 109 to 163 mm in width. All crabs 110 mm and over had

developing ovaries. One Eureka crab and 50 San Francisco crabs were under 110 mm. Fifteen San Francisco crabs had undeveloped ovaries typical of immature female crabs. All of the remaining crabs under 110 mm, including the smallest crab, had functioning ovaries. Because of a lack of Eureka crabs under 110 mm in the samples and the presence of both immature and mature San Francisco crabs in this size category, only those crabs 110 mm and over were used in comparisons of ovary maturity and relative fecundity.

Ovary color was tested statistically as an index of ovary maturity. Mean diameters of developing ova probably would have been a better index of ovary maturity, but these measurements were begun late in the study whereas ovary color was recorded routinely from the beginning. A simple regression of mean diameters of developing ova on ovary color showed a good linear relationship with a coefficient of determination (r^2) of 0.72 ($P < 0.0001$). Therefore, ovary color was considered a useful index for comparisons of ovary maturity.

The Eureka crabs' ovaries in the June 1979 sample appeared to be less developed than those in both San Francisco and Eureka samples taken during June 1976–1978. No comparable San Francisco samples were collected in 1979, so the June 1979 Eureka sample was excluded from between-area comparisons and statistically compared separately by color and weight with earlier samples.

Regressions of ovary color on time showed similar slopes for each area which were not significantly different from each other ($P > 0.5$; Figure 87). This indicates that ovaries in the two areas developed toward spawning at similar rates.

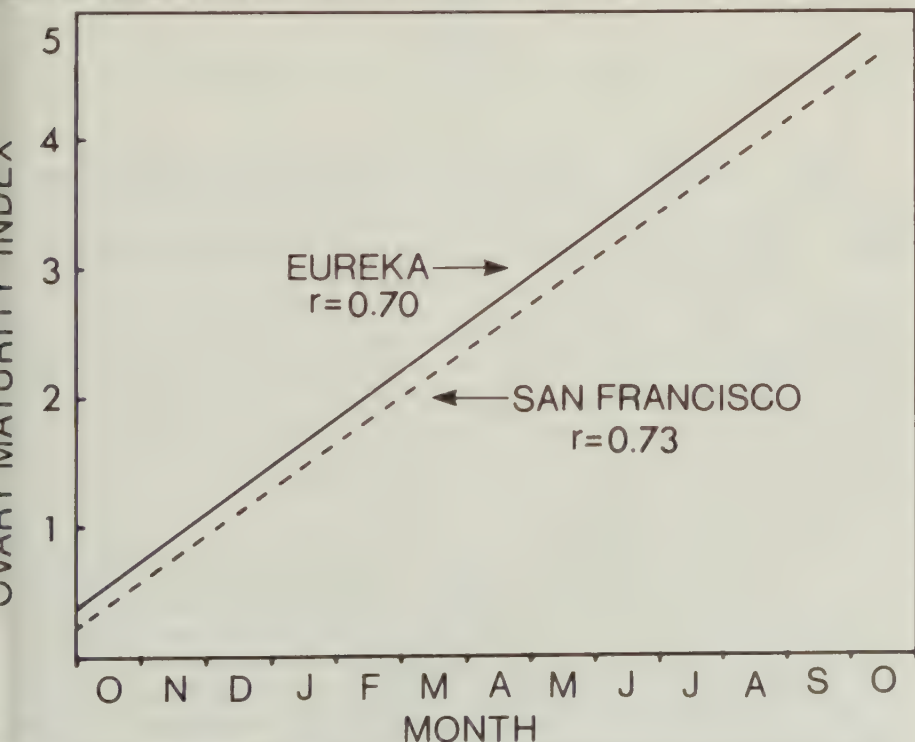


FIGURE 87. Regressions of ovary color on time for Eureka and San Francisco area crab ovaries during 1976–1979.

Overall, ovary weights ranged from a few tenths of a gram in early stages of development to 81.5 g in an ovary with well developed ova in mid-September. Ovary weights generally increased and the range in weights widened as the ovaries matured, although the range in ovary weights was greater in San Francisco than in Eureka area crabs (Figures 88 and 89).

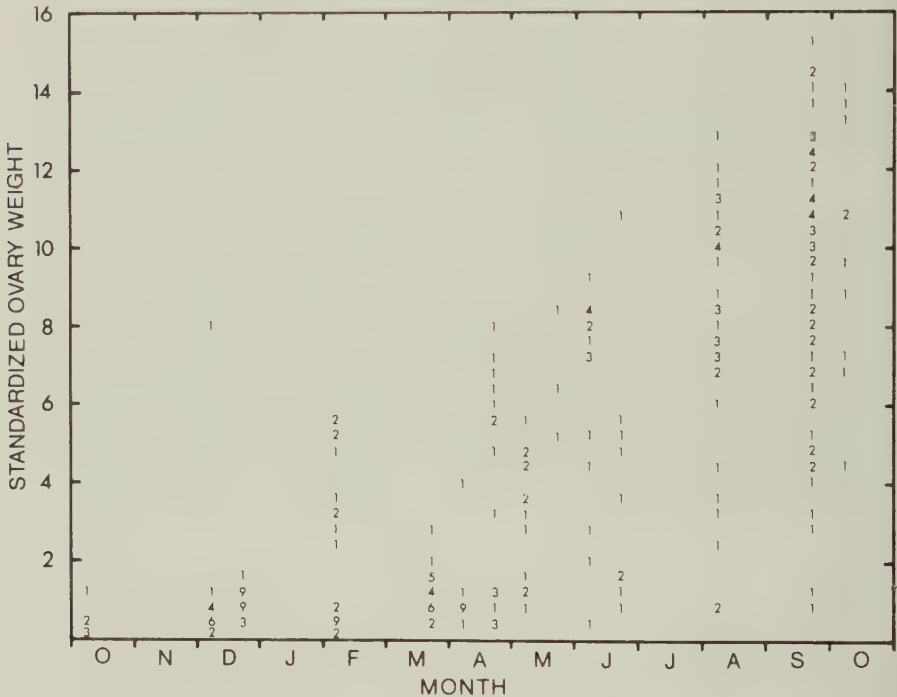


FIGURE 88. Standardized ovary weights in San Francisco area crabs plotted semi-monthly during 1976-1979.

A one-way analysis of covariance was carried out using ovary weights with area as a factor, and month and crab volume as covariates. The area effect was highly significant ($P = 0.001$). A multiple classification analysis showed a grand mean of 20.07 g. Eureka ovaries had a mean of 22.3 g and San Francisco ovaries a mean of 17.8 g. The overall coefficient of multiple determination (r^2) was 0.62. These tests indicate that crabs in the Eureka area produced more ovarian tissue than San Francisco area crabs.

Eureka ovaries from June 1979 (the only Eureka sample that year) were found to be significantly less developed compared to both San Francisco and Eureka ovaries during June 1976, 1977, and 1978. Non-parametric Kruskal-Wallis tests (Hollander and Wolfe 1973) indicated mean ova diameters, ovary color, and standardized ovary weights were all highly significantly different ($P = 0.02, 0.001, 0.0001$, respectively) between the June 1979 ovaries and all earlier Eureka and San Francisco June ovaries. In development, they appeared to be more similar to March and April crabs of the earlier years.

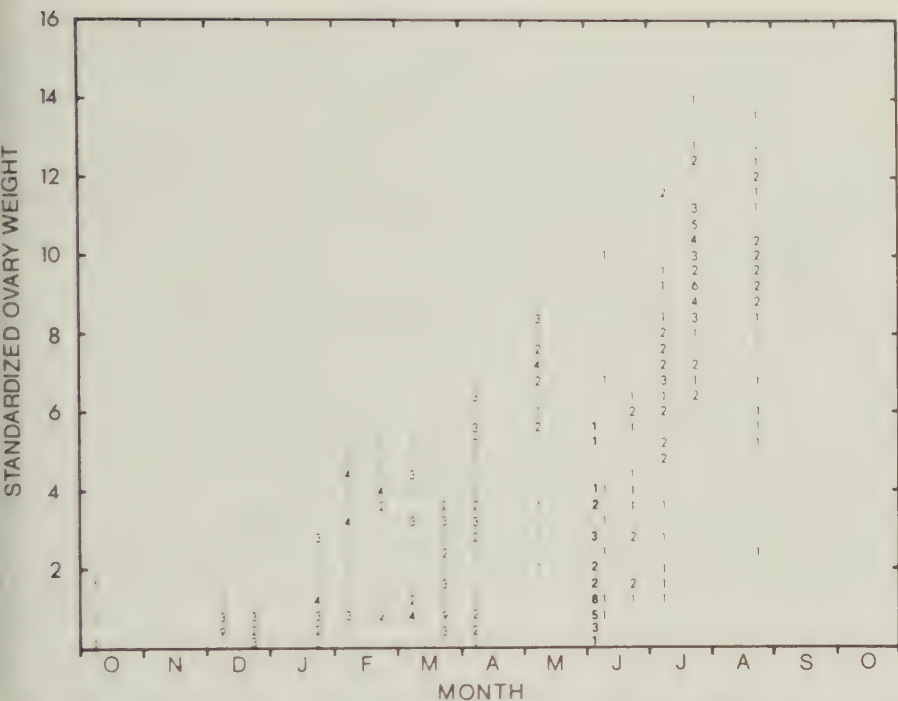


FIGURE 89. Standardized ovary weights in Eureka area crabs plotted semi-monthly during 1976-1979 (June 1979 ovaries are shown in bold-face numbers).

DISCUSSION AND CONCLUSIONS

The similar rates of ovary maturation which are indicated for both central and northern California are probably the result of the crabs responding to similar annual oceanographic cycles in both areas. The annual oceanographic cycle in the California Current region includes an upwelling period during spring and summer months, an oceanic period during the fall, and the Davidson Current period during the winter (Bolin and Abbott 1963). Although there are some local differences due to coastal topography, localized wind and weather conditions, river runoff, etc., the main difference in the oceanographic climate in these areas is that ocean temperatures are cooler progressively northward along the coast.

This study shows that crab ovaries begin redeveloping soon after spawning while the crabs are still brooding their eggs. This is probably an important factor in the similarity of maturation rates. Spawned, fertilized eggs develop more slowly in colder water (Wild, Chapter 16) and if ovaries did not begin redeveloping until after the eggs hatched, significant differences in ovary development rates between areas might be expected.

The relatively smaller ovaries produced in central California could be related to one or several factors such as fewer ova, smaller ova, or less interstitial material being produced. Although crabs in the laboratory in seawater at 17 C (warmer than normal for these crabs) spawned smaller eggs than crabs in 14 and 10 C seawater (Wild, Chapter 16), differences in egg size were not so apparent between the two lower temperatures which are closer to ocean tem-

peratures in central and northern California. Therefore, the most likely explanation is that crabs in central California produced fewer ova, overall, which would have resulted in a relatively lower fecundity for that population.

The delayed ovarian development in Eureka area crabs in 1979 was very likely due to anomalously colder ocean temperatures which persisted along the coast during the late winter, spring, and summer of 1979 (NOAA, Fishing Information Reports). This delayed ovarian development also may have been related to delayed spawning observed in Eureka area crabs brought into the laboratory that year (Wild, Chapter 16).

Female crab fecundity probably reflects physiological responses to environmental conditions of which ocean temperature is an important feature. The crabs, being poikilothermic animals, would be expected to have higher metabolic rates at warmer temperatures which could result in less energy being available for ovary production. Thus, warmer ocean periods, particularly in more southern areas of the crabs' range, such as in central California, could result in lowered fecundity. Lower fecundity, added to greater mortality of fertilized eggs in warmer water (Wild, Chapter 16), and (or) poor survival of larvae and juveniles could be at least partly responsible for the long-term decline in commercial crab landings in central California which occurred during a period when ocean temperatures, on the average, were higher (Wild et al., Chapter 14).

Chapter 16

THE INFLUENCE OF SEAWATER TEMPERATURE ON SPAWNING, EGG DEVELOPMENT, AND HATCHING SUCCESS OF THE DUNGENESS CRAB, *CANCER MAGISTER*

by

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INTRODUCTION

Adult female Dungeness crabs undergo an annual cycle of molting, mating, spawning, egg brooding, and hatching larvae. An understanding of how these life history phenomena respond to variations in the environment is necessary in analyzing effects of the environment on population fluctuations and fishery landings. One of the more important environmental variables affecting marine organisms is seawater temperature.

Some information is available on effects of seawater temperature on various crab life history phenomena. Thermal tolerances and responses of adult Dungeness crabs to seawater temperature were studied by Prentice (1971) and Mayer (1973). Reed (1969) analyzed effects of temperature and salinity on growth and survival of Dungeness crab larvae. However, very little information is available on effects of seawater temperature on the various aspects of Dungeness crab reproduction. Mayer (1973) studied short-term effects of seawater temperature on survival of Dungeness crab eggs removed from the females' pleopods.

The objective of the present laboratory study was to examine effects of seawater temperature on spawning, egg development, and hatching success of female Dungeness crabs from central and northern California so that these factors could be analyzed for relationships to crab population fluctuations.

DUNGENESS CRAB REPRODUCTIVE BIOLOGY

In California, most Dungeness crab mating occurs in the spring from about March through June. Mating occurs between a hard-shelled male and a newly-molted, soft-shelled female (Snow and Neilson 1966). Sperm are stored internally in the female's paired spermathecae until spawning which usually occurs in the fall from late September to November in California. The eggs are fertilized as they pass through the reproductive tract at the time of spawning and are extruded through paired ovipores on the crab's sternum. The eggs form a sponge-like mass (Figure 90) as they adhere individually to the pleopodal hairs on the crab's abdomen where they are brooded until they hatch. A crab must be at least partially buried in sand for the egg mass to form. An egg mass may contain as many as one to two million eggs. Egg masses are usually bright orange



FIGURE 90. Female Dungeness crab with egg mass. Photo by Paul W. Wild.

in color when spawned and gradually change to dark brown as the developing embryos deplete the yolk and pigmentation and eye spots appear before hatching. Most egg brooding (ovigerous) crabs generally are found in central California from about October through December and in northern California from about October through January. Ovigerous females are found even later in the year on up the coast where temperatures are cooler and the egg brooding period is longer. Hatching in central California usually occurs from late December to early February and in northern California from January to early March.

METHODS AND MATERIALS

Adult female Dungeness crabs were collected from both San Francisco and Eureka areas (central and northern California, respectively) during late May, June, or July of 1977, 1978, and 1979 and transported to the Department's Marine Culture Laboratory near Monterey, California. Crabs which had obviously molted recently, and thus presumably had mated, were selected at the laboratory for the experiments. Twenty crabs were used in 1977, 24 in 1978, and 24 in 1979. These crabs ranged in size from 130 to 156 mm in carapace width (excluding the 10th anterolateral spines).

The crabs were held in separate compartments in fiberglass aquaria, four crabs (two from each area) in each aquarium. The aquaria were equipped with sand and aerated sub-sand filters and were supplied with seawater in an open (non-recirculating) system. The seawater was pumped from the ocean nearby, filtered, and ultraviolet-treated at the laboratory.

Three seawater temperature regimes were used each year including one at approximately 17 C, one at approximately 10 C, and one at ambient which, fluctuating between the other two, averaged 13–14 C during the experiments.

Ambient laboratory temperature approximated ocean temperature off San Francisco while the other two were respectively higher and lower; the lower regime was closer to conditions off Eureka. The crabs were maintained at these temperatures during prespawning, spawning, egg brooding, and hatching periods.

Each experiment began with eight crabs in each temperature regime, except in 1977 when only four crabs were held in ambient. Also in 1977, air and seawater supplies to one warm aquarium malfunctioned and all four crabs died before spawning, leaving only four crabs to spawn in warm seawater that year.

At least three times per week, throughout each experiment, seawater temperatures were monitored, crab behavior was noted, and the crabs were fed. Food consisted of frozen market squid, *Loligo opalescens*, diced before feeding, and frozen Pacific ocean shrimp, *Pandalus jordani*.

During all three experiments, time of spawning, condition and color of the egg masses, and time of hatching were recorded. During 1978 and 1979, egg mass volumes were measured periodically and estimates of numbers of larvae hatched were calculated by serial dilution and counting. Egg mass volumes were obtained by removing a crab from an aquarium, gently pressing seawater from the egg mass, and forming aluminum foil over it to form a cup. The cup was removed and filled with seawater which was then measured in a graduated cylinder. The mean of about five repeated fillings was recorded as the volume. Of several methods considered, this method, although somewhat imprecise, was the least traumatic to crabs and egg masses, allowed for periodic measurements, and gave values which were useful in comparisons of egg mass volumes within and between seawater temperatures.

Periodically during the 1979–80 experiment, observations were made on conditions in the egg masses, developmental stages of the eggs recorded, and egg diameters measured. For these observations, approximately 1000 to 3000 eggs were removed with forceps from an egg mass and examined under a dissecting microscope. Associated organisms and condition of eggs and the egg mass in general were noted. Egg diameters were measured for approximately 25 eggs per sample at 100x magnification under a compound microscope equipped with an ocular micrometer.

During the 1979–80 experiment, a separate, small scale experiment was run to obtain information on the relationship between crab eggs and a nemertean worm *Carcinonemertes errans*, which lives in the egg mass. An apparatus was devised with five cells to hold crab eggs with varying densities of worms in continuously flowing seawater (Figure 91). The system was maintained in seawater at ambient temperature (mean, approximately 13.5 C) for about 60 days.

RESULTS AND DISCUSSION

Spawning

All spawnings occurred between mid-September and early December, although most occurred before mid-November. A few crabs died before spawning, but all of the remaining crabs spawned during this period (Figure 92). Nonparametric Kruskal-Wallis tests (Hollander and Wolfe 1973) were used to determine the significance of differences in dates of spawning by year, location, and temperature.

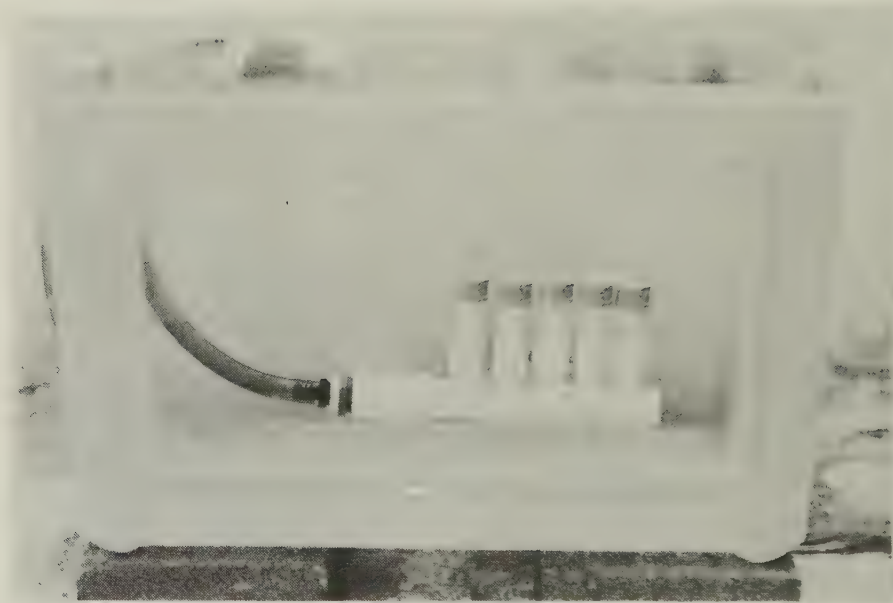


FIGURE 91. Apparatus for crab egg and nemertean worm experiments. Nitex screening (90- μ m mesh) was glued to tops of cell caps and lower ends of cells. Seawater circulates through cells by venturi action.

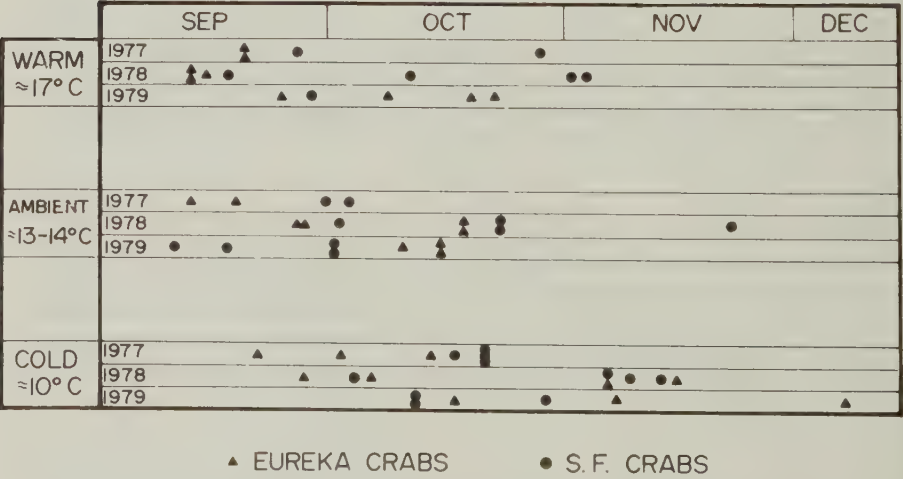


FIGURE 92. Spawning dates of female Dungeness crabs at various seawater temperatures in the laboratory.

There were no significant differences in dates of spawning by year within temperature regimes, except in ambient seawater where the differences were only slightly significant ($P = 0.076$) with spawning dates tending to be later in 1978.

When all temperature regimes within each year were considered together, there was a tendency for Eureka area crabs to spawn earlier than San Francisco crabs in both 1977 ($P = 0.008$) and 1978 ($P = 0.045$), while in 1979 there was a tendency for San Francisco crabs to spawn earlier ($P = 0.041$).

There appeared to be a trend towards crabs spawning later in colder water. However, Dunn's multiple comparisons (Hollander and Wolfe 1973) show that spawning dates were not significantly different between ambient and warm regimes, but were significantly different between cold and ambient and cold and warm regimes with an experimental error rate of 0.05. Therefore, crabs in the coldest temperature tended to spawn later than in both ambient and warm regimes.

One additional observation of interest is that spawning dates of San Francisco crabs in ambient seawater were not significantly different from Eureka area crabs in cold seawater ($P = 0.19$). In both cases the crabs were in temperatures approximating their natural environments. This suggests that crabs in San Francisco and Eureka areas may tend to spawn at similar times.

The reversal in spawning trends by areas in the 1979 experiment may be due to differences in maturation rates of ovaries in crabs in the two areas. Ovaries in Eureka area crabs in June 1979 were considerably delayed in development compared to ovaries in both San Francisco and Eureka area crabs in 1976–1978 (Wild, Chapter 15). San Francisco crab ovaries were not examined in 1979, but the laboratory results indicate that they matured earlier than Eureka crabs that year.

Egg Brooding Period

Differences in average egg brooding temperatures from year to year produced differing egg brooding periods even within regimes. The warmest regime averaged 16.7 C for all 3 years and varied the least in egg brooding periods. Average ambient egg brooding temperatures ranged from 12.9 C in 1978 to 13.9 C in 1979. Cold egg brooding temperatures averaged 9.4 C in 1977 and 10.0 C in 1978 and 1979. The egg brooding periods varied inversely with these seawater temperatures (Figure 93). The prolonged egg brooding periods in colder water are consistent with prolonged occurrences of ovigerous crabs and cooler ocean temperatures progressively northward along the coast.

Egg Development

The eggs were usually bright orange in color when spawned and began to undergo cell division soon after spawning. After several days cell division had proceeded to the blastula stage and division continued until the eggs appeared to be full, granular, orange yolks. The developing embryo was first apparent as a small clear area in the yolk at the periphery of an egg. As the embryo developed it became observable from a lateral view as a transparent crescent over the yolk. As the embryo continued to grow and absorb yolk, faint lines and spots of purplish pigmentation eventually appeared on the dorsum of the embryo, followed shortly by tiny black eye spots on the head. As development progressed, the pigmentation darkened, the eye spots enlarged, and the yolk was entirely absorbed by the time the embryo was ready to hatch.

At about 10 C, early cell division to the blastula stage usually took about 7 to

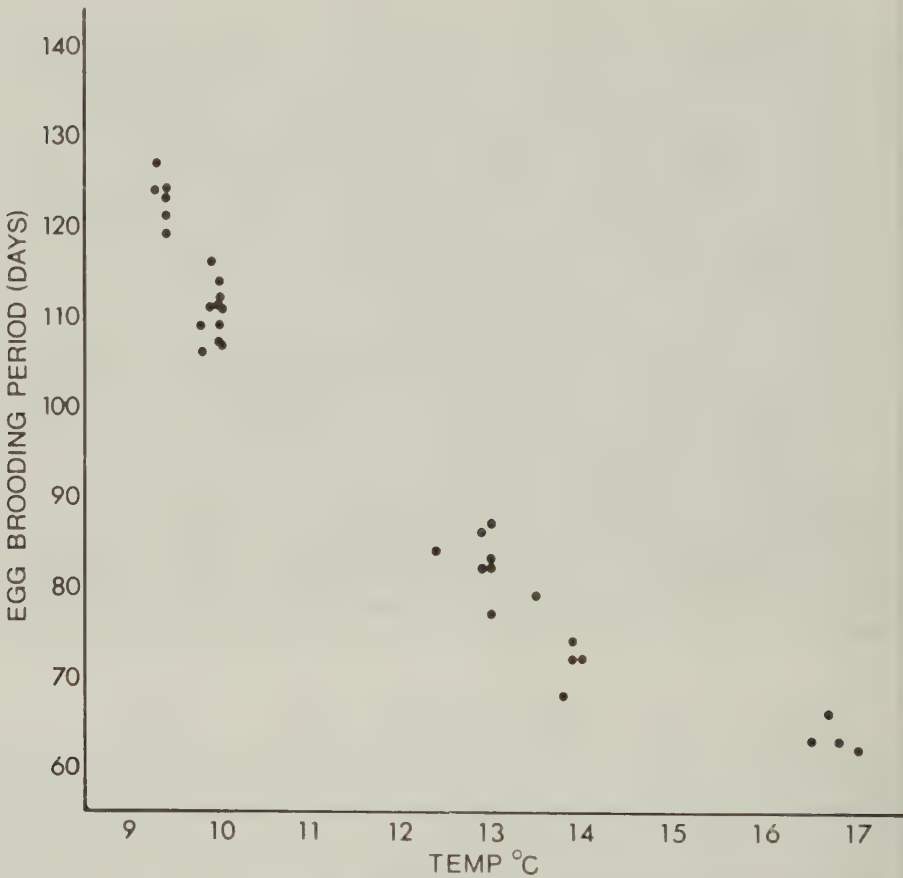


FIGURE 93. Dungeness crab egg brooding periods at laboratory seawater temperatures.

10 days. The granular appearing yolk usually was apparent by 2 weeks and the small clear area of the developing embryo usually became apparent at about 40 days. Faint pigmentation and eye spots were visible at about 80 days. Hatching occurred on the average at about 110 days.

Because of faster development in warm and ambient seawater and the infrequency of observations, time of appearance of these stages was not as apparent. However, by considering timing of the stages in cold water as percentages of the total egg brooding period, the expected timing in warm and ambient seawater, with mean hatching times of 64 and 72 days, respectively, would be as follows: completion of early cell division—3 to 6 and 4 to 7 days; granular appearing yolk—8 and 9 days; small clear area of early developing embryo—23 and 29 days; faint pigmentation and eye spots—46 and 52 days. Although observations rarely were made right at these times, the development observed between the expected times supports the expected pattern well.

Egg diameters (measured only in the 1979–80 experiment) increased in size as the eggs developed toward hatching (Figures 94, 95, 96). Mean egg diameters

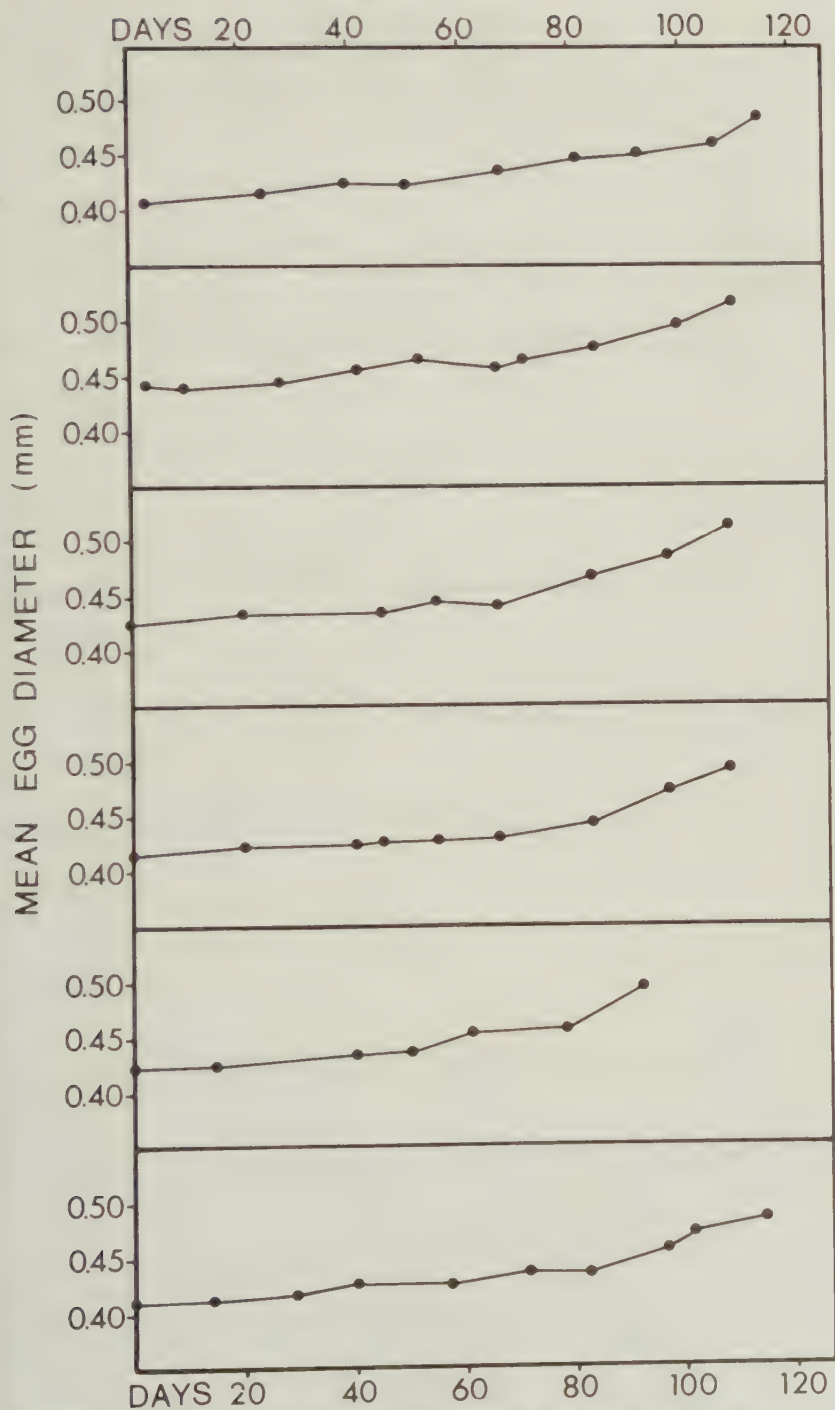


FIGURE 94. Diameters of developing eggs in six Dungeness crab egg masses at approximately 10 C. Each data point equals mean of approximately 25 eggs.

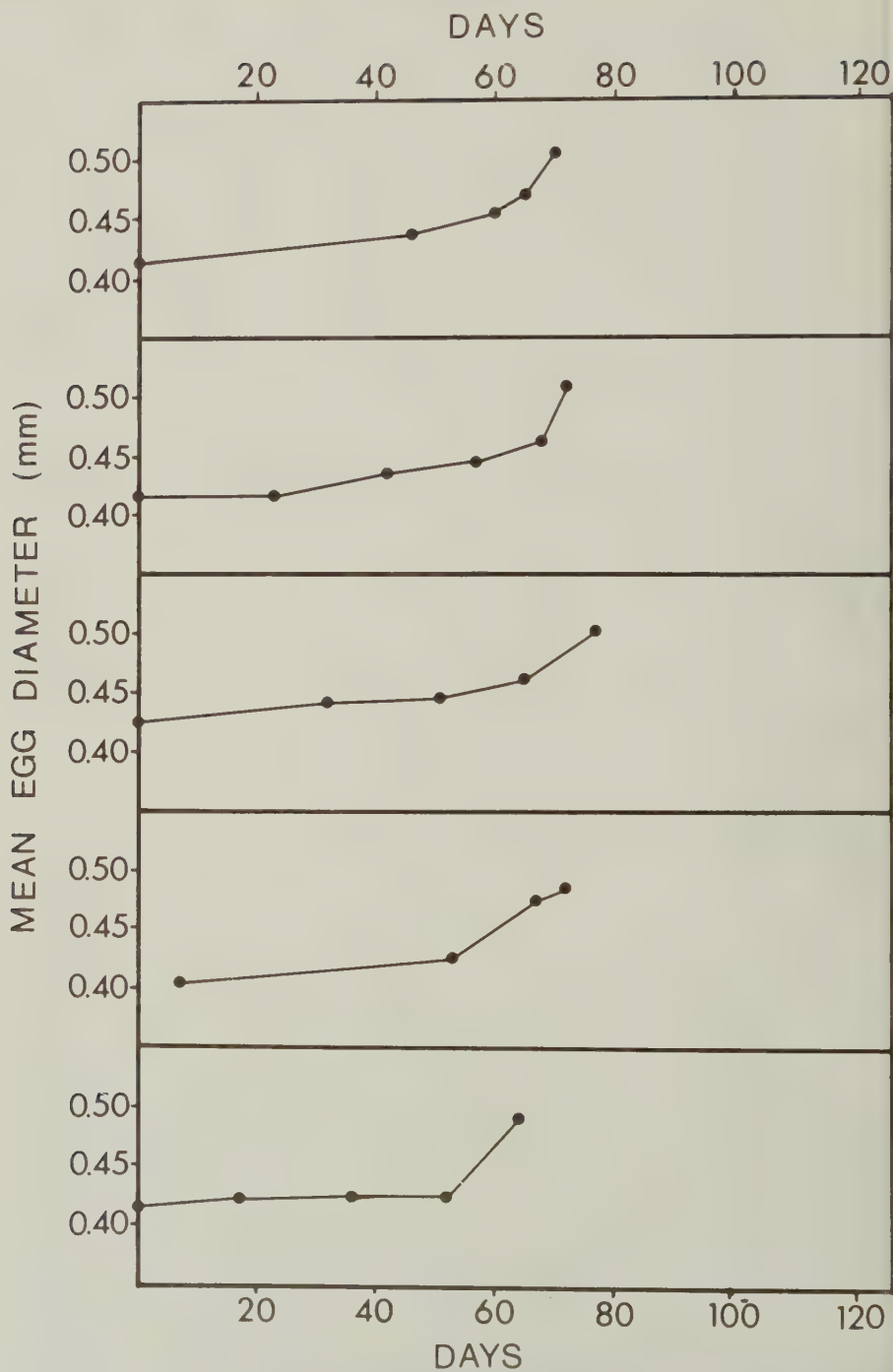


FIGURE 95. Diameters of developing eggs in five Dungeness crab egg masses at approximately 14 C. Each data point equals mean of approximately 25 eggs.

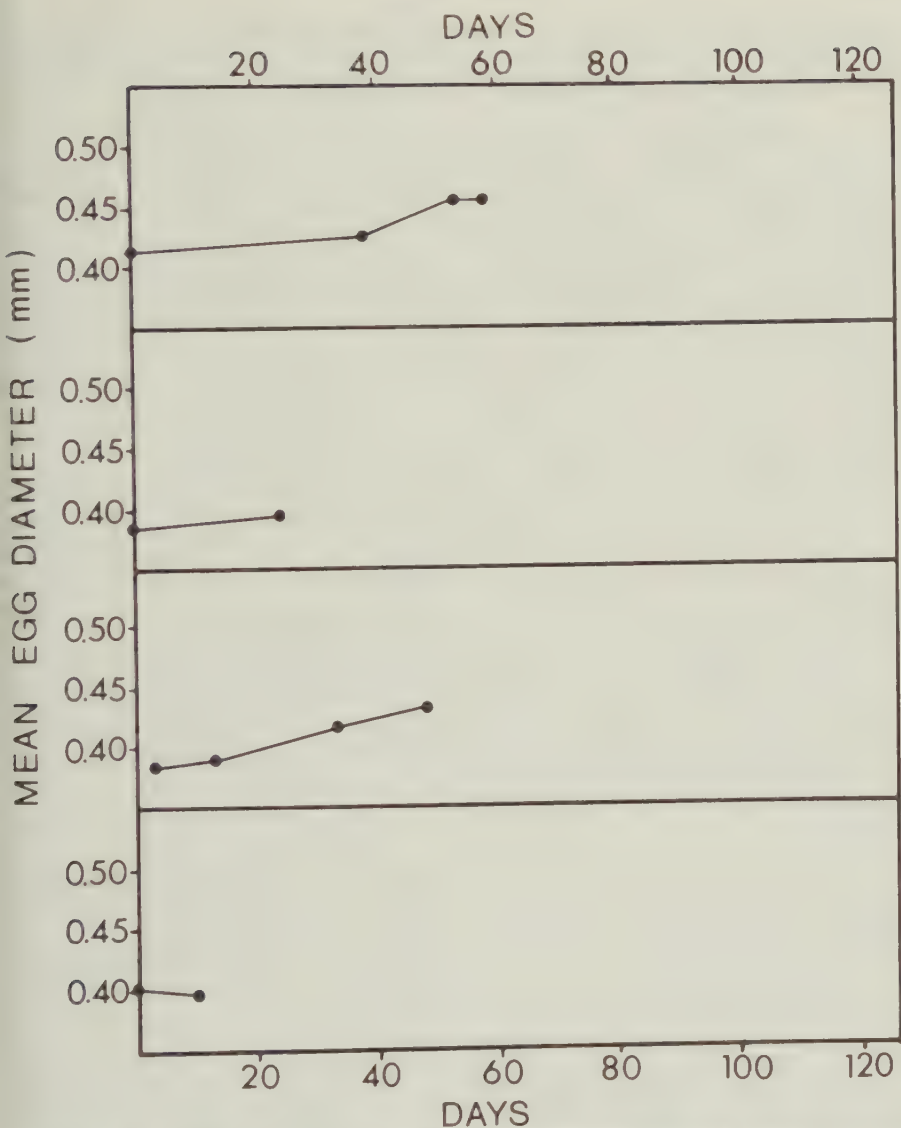


FIGURE 96. Diameters of developing eggs in four Dungeness crab egg masses at approximately 17 C. Each data point equals mean of approximately 25 eggs.

in samples of newly-spawned eggs averaged 0.39 mm in warm seawater, 0.41 mm in ambient, and 0.42 mm in cold. These means were significantly different only between warm and ambient and warm and cold regimes (Students t-test, $P < 0.05$), while the differences between ambient and cold were not significant ($P > 0.10$). However, these results are not conclusive because there were too few samples to analyze adequately for trends. During this experiment (1979–80), only one egg mass in warm seawater had a few eggs survive to hatch, at which time the mean egg size was 0.46 mm, with a range of 0.42 to 0.49 mm.

Mean egg diameters at hatching in both ambient and cold were 0.50 mm (0.497 and 0.500, respectively). Again, the number of egg masses sampled was too few to determine significance or trends.

Organisms and Conditions Observed in Egg Masses

A variety of organisms was observed in samples of the egg masses. The most commonly observed organisms were copepods, the nemertean worm *Carcinonemertes errans*, and nematodes. Occasionally, a polychaete, or other type of worm, or hydroids were observed. At higher magnification (100x), a filamentous bacterium, presumably *Leucothrix mucor* which is known to infest crustacean eggs (Johnson et al. 1971) frequently was observed on the surface of eggs, at times in dense concentrations. Whether this bacterium causes mortality of Dungeness crab eggs is not certain, but a close association of microbial fouling and mortality of Dungeness crab eggs has been reported (Fisher 1976). Nevertheless, in the present experiment live and apparently healthy larvae hatched from egg masses with fairly heavy infestations of these bacteria.

Empty egg membranes and dead eggs were often observed in the samples. The interior of dead eggs often appeared cloudy white. These eggs were often larger than normal, as if undergoing bacterial action, and some apparently had burst. Sometimes dead eggs were observed with whitish bumps (possibly bacterial colonies) over their surfaces. These deteriorating conditions generally appeared to be more prevalent the warmer the water. Empty egg membranes were often abundant at the surface of the egg masses, particularly in the anterior area. It seems possible that abrasion of the egg mass during burying and unburying by the female crab could be responsible for some of this peripheral mortality.

Copepods and nemerteans usually were observed throughout the egg brooding period. The nematodes were observed more often after empty egg membranes were present and these small worms were often seen inside empty egg membranes.

Usually only a few copepods were observed in the samples and no attempt was made to count them. The number of nemerteans was noted in most of the samples along with an estimate of the number of crab eggs. Usually only one or two worms per 1000 crab eggs were observed. However, as the egg masses deteriorated and became smaller in size, worm densities increased, presumably because the worms were concentrated among fewer eggs. One count of about 20 worms per 1000 crab eggs was recorded.

The nemerteans, *C. errans*, lie dormant in creases and crevices on Dungeness crab exoskeletons prior to spawning. There is evidence that nemertean worms may transfer from male to female crabs during mating (Kuris 1971). When the female crabs spawn, the worms migrate to the egg masses where they complete their life cycle, including mating and laying their eggs among the crabs' eggs. The worm's eggs are much smaller than the crab's eggs and are laid in elongate clusters. Nemertean larvae began hatching prior to and during crab egg hatching. On one occasion I observed worm larvae hatching 3 weeks before the crab's eggs hatched, although worm hatching usually began only 1 or 2 weeks before crab eggs began hatching.

Wickham (1979a, 1979c, 1980) describes *C. errans* as a crab egg predator and considers it responsible for the decline in the central California crab fishery. In hundreds of observations of these worms, I have been unable to determine

whether they actually eat crab eggs. Wickham (1980) reported lower infestation rates in northern California crab egg masses than in central California. All of the crabs I brought into the laboratory presumably had infestations typical of these two geographic areas, but there were no apparent trends in egg mortality by area in my experiments. The egg mortality I observed, and that in a short-term experiment by Mayer (1973), appear to be related to seawater temperature. Whether the temperature effect is direct or indirect (i.e., increased bacterial fouling, predation, etc.) was not apparent. Nevertheless, both crab eggs and worms develop faster at elevated temperatures, which probably means that the total cumulative metabolic requirement for the worms may not be too different at the various temperatures. Thus, even if predation does occur, it would not account for the increased egg mortality observed in warmer laboratory temperatures.

Furthermore, several crabs in the laboratory, primarily in warm and ambient seawater, without molting or mating spawned second egg masses in which virtually no worms were found. These egg masses deteriorated similarly to the other egg masses. The lack of worms in these egg masses suggests that the worms either die or are unable to reinfest the eggs.

Hatching Success

Although the eggs developed faster at warmer seawater temperatures, conditions in the egg masses deteriorated, egg mortalities increased, and egg mass volumes declined in both warm and ambient regimes (Figures 97 and 98). As a result, hatching success (number of larvae hatched from an egg mass) decreased as temperature increased. The egg mass volumes declined even though surviving eggs increased in size from about 0.4 mm in diameter to 0.5 mm by the time they hatched. The increase in egg size resulted in increasingly larger egg mass volumes in the coldest temperature (Figure 97) in which egg mortalities were lowest and hatching success was highest.

Problems with a new seawater intake pump in late December 1979, after most hatching was completed in warm and ambient seawater, apparently caused increased egg mortalities which resulted in declining egg mass volumes and low hatching success in cold seawater in 1979–80 (Figure 98). Air leaks on the suction side of the pump caused the seawater to become super-saturated with nitrogen. The pump was shut down for about 30 hr for repairs which resulted in reduced seawater flow and a temporary rise in laboratory seawater temperatures. Other laboratory animals including abalones, clams, crab larvae, etc., experienced high mortalities at this time, presumably from nitrogen bubble disease (Earl Ebert, Calif. Dep. Fish and Game, pers. commun.) which also has been encountered in lobster culture (Hughes 1975). Some delayed mortality in adult crabs was attributed to the pump problems.

The average number of larvae hatched per egg mass in 10.0 C seawater in 1978–79 was 685,000. Increased mortality associated with the pump problems in late 1979 precluded evaluating hatching success related to egg survival and development in cold seawater in the 1979–80 experiment. In ambient seawater at 12.9 C in 1978, an average of 257,000 larvae per egg mass hatched, and in 1979 at 13.9 C, the average was 292,000. The overall average for ambient was 275,000. In the warmest regime at 16.7 C in both 1978 and 1979, the only egg mass which produced any significant amount of larvae hatched approximately

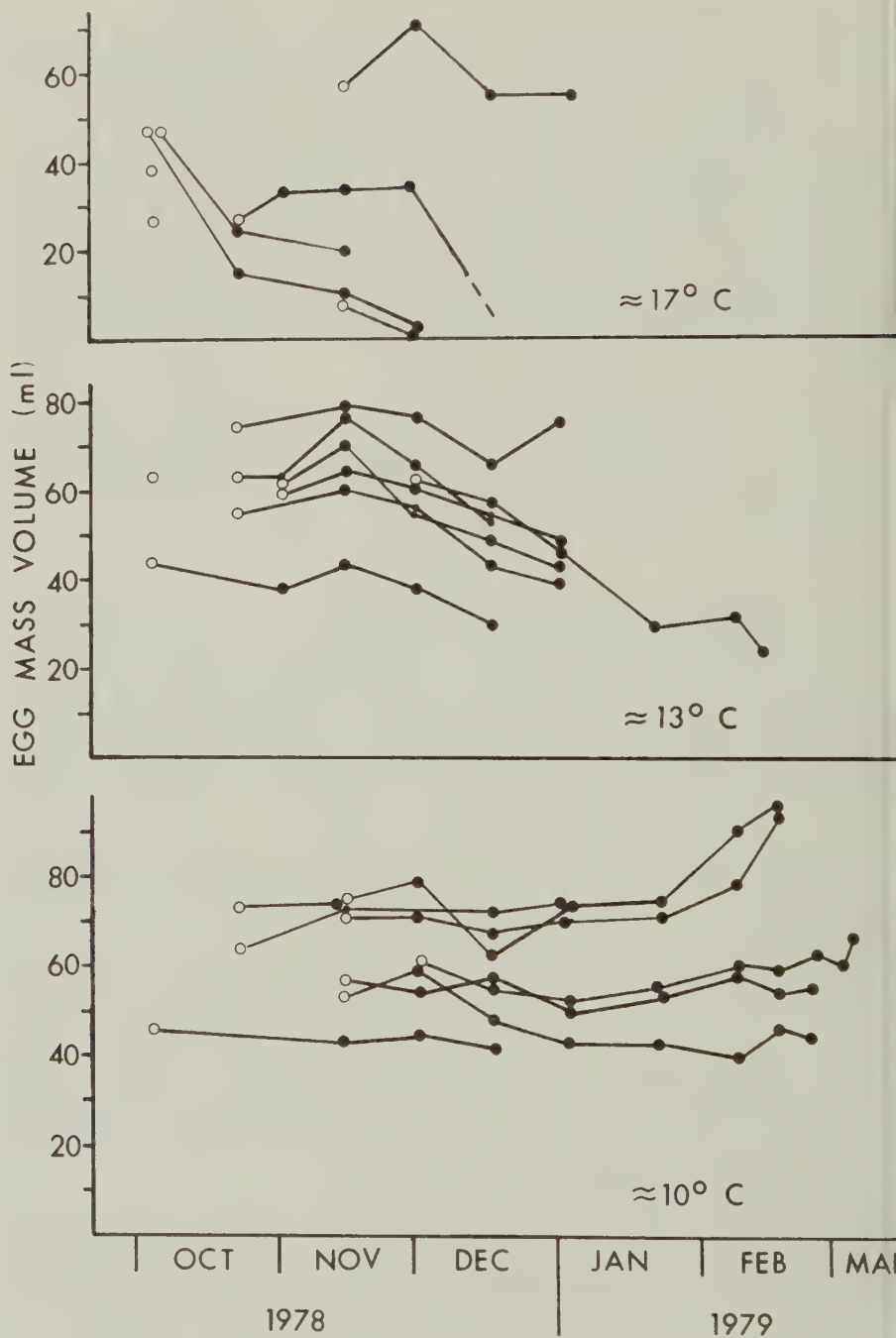


FIGURE 97. Progressive volumes of individual Dungeness crab egg masses at various laboratory seawater temperatures, 1978-79.

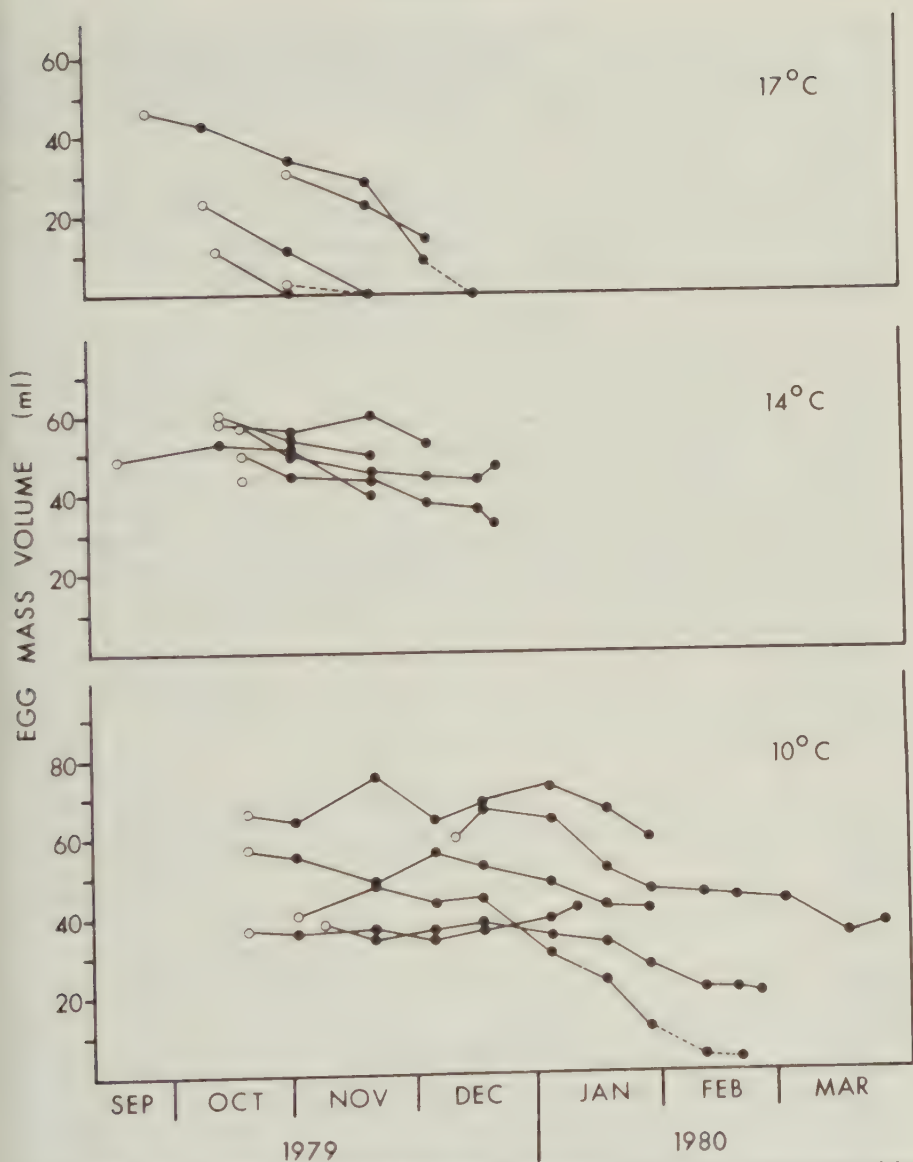


FIGURE 98. Progressive volumes of individual Dungeness crab egg masses at various laboratory seawater temperatures, 1979-80.

110,000, at least half of which died shortly after hatching. Overall, the average hatch per egg mass in warm seawater was 14,000, but virtually no larvae hatched from most of these egg masses. These data suggest that a temperature of about 16.0 to 17.0 C may represent an upper lethal limit for developing Dungeness crab eggs.

In a study near Puget Sound, Washington, Mayer (1973) observed effects of seawater temperature on Dungeness crab eggs removed from females' pleopods

and cultured at 5, 10, 15, and 20 C for about 15 days. Egg mortalities during this relatively short period were minimal at 5 C, reached about 20% at 10 C, showed "a significant increase in the slope of the mortality curve at 15 C due to the effect of elevated temperatures between 10 and 15 C," and at 20 C, 100% mortality occurred in about 6 days.

These laboratory studies, therefore, indicate that seawater temperatures which have occurred in central California (Wild et al., Chapter 14) could adversely affect egg survival and hatching success and, thus, could have been a factor in the decline of Dungeness crab fishery landings.

Adult Crab Survival

Collecting and transporting crabs is stressful to them and may have contributed to some early crab mortality in my experiments. However, mortalities occurred throughout the experiments and, with all 3 years considered together, were higher at the warmer temperatures (Figure 99). After approximately 8 months, only 20% of the crabs in warm seawater were alive, while 42% in ambient and 65% in cold seawater survived. Excluding the mortality in cold seawater apparently associated with intake pump problems in 1979-80 (Figure 99), survival in cold water was 83%. These results suggest that seawater temperature was a major factor affecting crab survival in the laboratory.

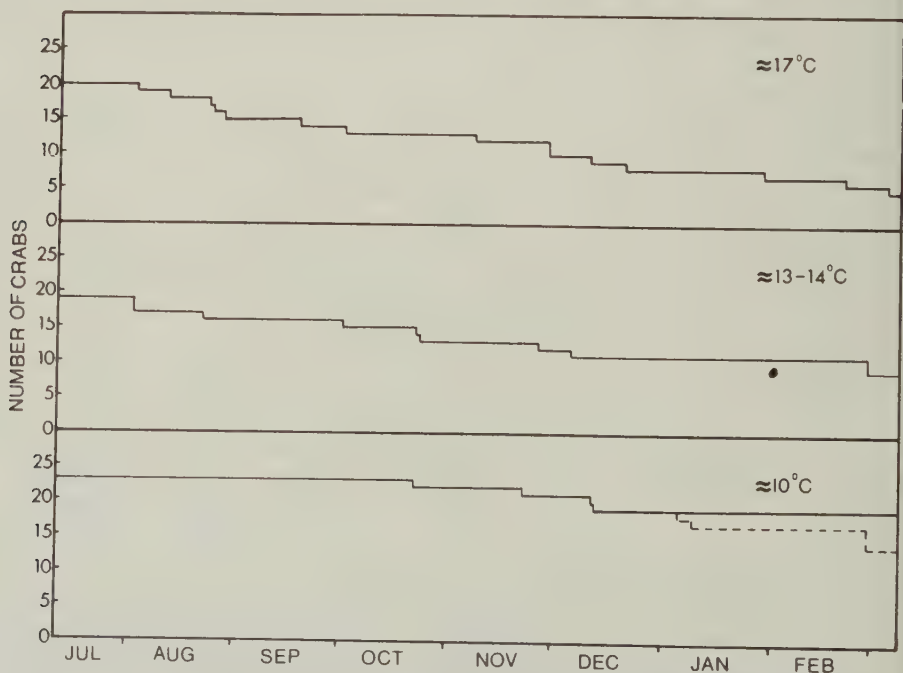


FIGURE 99. Female crab mortality in three laboratory temperature regimes during July-March 1977-78, 1978-79, and 1979-80. Dashed line at 10 C represents mortality associated with seawater intake pump problems in 1979-80.

If seawater temperature affects survival and average life span similarly in crab populations in the ocean, unusually warm conditions in central California (Wild

et al., Chapter 14) could have resulted in a reduction in adult spawning stock. Such a reduction in spawning stock combined with increased egg mortality would make it difficult for the crab population to recover even during the brief periods of more favorable conditions which have occurred in recent years.

Additional Information on Nemertean Worms and Crab Eggs

Wickham (1979a, 1979c) experimented with the nemertean worm *Carcinonemertes errans* and Dungeness crab eggs in darkened test tubes at densities of 0, 1, and 2 worms per 50 crab eggs for 10 days. He reported increasingly greater fouling and egg mortality in test tubes with worms. However, because of the relatively long brooding period of Dungeness crab eggs, it is important to be able to observe such relationships for a much longer period and this requires a system which provides continuous seawater circulation over the eggs and worms.

In late 1979, I planned a small-scale experiment to develop and test a system for maintaining crab eggs apart from the female for long periods of time and to obtain some preliminary data on *C. errans* and crab eggs. On January 3, 1980, the experiment was begun with 0, 2, 4, 6, and 8 worms per 100 to 106 crab eggs in individual cells in a flow-through seawater system (Figure 91). The eggs were left on the setae to which they were attached when removed with forceps from the egg mass. The egg mass had been brooded in 10 C seawater for about a month. The experiment was run in seawater at ambient laboratory temperature (about 13.5 C) for 60 days. No replicates were run in this preliminary experiment. Observations were made at intervals of 3 to 8 days by emptying eggs and worms into a watch glass and viewing them under a dissecting microscope. Some worms at times remained and were observed in the cells when the eggs were removed.

Unfortunately, this experiment began about the time the aforementioned seawater pump problems occurred. Because of this and the preliminary nature of the experiment, the results must be interpreted cautiously. Nevertheless, some larvae eventually hatched in this experiment, which suggests that this type of system could be useful in future experiments. It is primarily for this reason that the results are presented here.

High mortality of crab eggs occurred in all cells during the first 10 to 15 days and then generally tapered off (Figure 100). Egg masses in cold seawater, the last of which to spawn was the source of eggs for this experiment, concurrently experienced increased egg mortalities evident in declining egg mass volumes (Figure 98). Most of this mortality presumably was due to unfavorable seawater conditions associated with the pump problems. Although ambient seawater temperature presumably caused some additional egg mortality in the cells, I saw no mortality that I could interpret as being caused by nemertean worms eating eggs.

Overall, egg survival and hatching were best at the two highest worm densities. In all, 14 crab larvae hatched; a total of 1, 8, and 5 larvae hatched in the cells with beginning worm densities of 2, 6, and 8 worms, respectively (Figure 100). Hatched crab larvae were observed on days 53, 56, and 60, and ranged from dead prezoeae to live, apparently healthy, first stage zoeae. The larvae were removed from the cells as they were found so that they would not be confused with subsequent hatching.

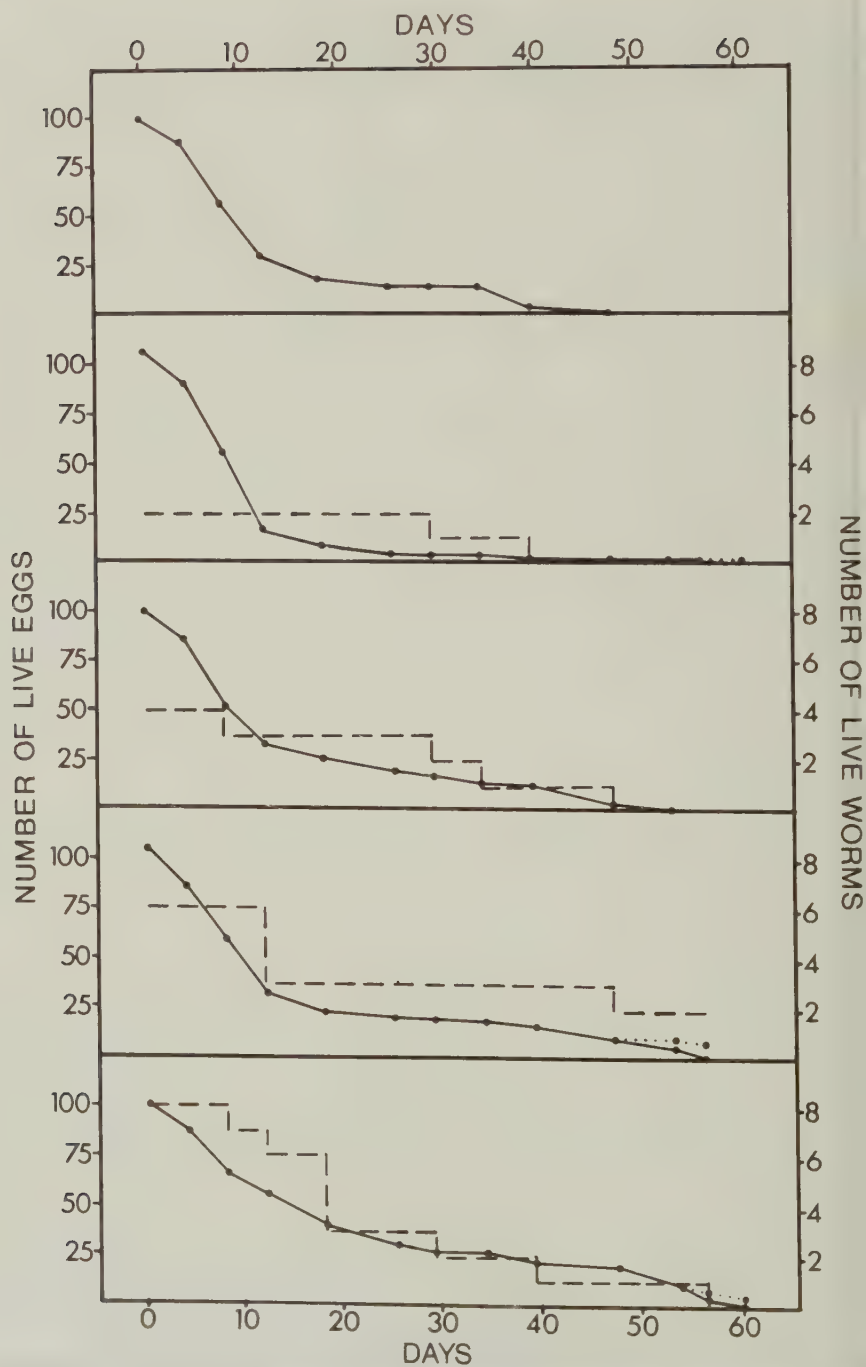


FIGURE 100. Mortality of Dungeness crab eggs and nemertean worms in individual cells in the laboratory. Solid line = live crab eggs; dashed line = live worms; dotted line = hatched crab larvae plus live eggs.

Worm mortality also occurred in the cells, but higher worm densities generally remained so throughout the experiment (Figure 100) and some clusters of worm eggs eventually were laid. Worm egg clusters were found only in the eight-worm cell. One egg cluster was observed on the 47th day and three were seen on the 56th day.

Other conditions in the cells were similar to those observed in samples from egg masses including occasional copepods, nematodes (sometimes in empty eggs), filamentous fouling, cloudy eggs, and whitish bumps on dead eggs. Filamentous fouling (fuzzy appearing eggs at low magnification) was, in general, more apparent on dead eggs but, overall, was least apparent at the higher worm densities.

Results of this experiment demonstrate that crab eggs and worms can be maintained apart from female crabs for long periods and apparently undergo normal development. Furthermore, with this system controlled temperature experiments with exact numbers of worms and eggs can be conducted, something not possible with whole egg masses. Such experiments are needed to provide more specific information on relationships between Dungeness crab eggs, nemertean worms, and environmental conditions to more fully understand crab population fluctuations and to make proper management recommendations.

Chapter 17

THE EFFECTS OF CHLORINATION OF WASTEWATER ON JUVENILE DUNGENESS CRABS IN SAN FRANCISCO BAY WATERS

by

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INTRODUCTION

In the minds of many the increased pollution of San Francisco Bay-Delta waters is implicated in the decline in catches of Dungeness crabs, *Cancer magister*, off San Francisco (Figure 10). The discharge of domestic and industrial waste into the Bay-Delta obviously has increased with population but was not well documented in the first half of this century. Since 1960, due to regionalization of sewage collection, waste loads directly discharged into the Bay have increased at a faster rate than population growth. However, due to better treatment, pollutants that increase biological oxygen demand (BOD), other than those related to chlorination, have decreased (Figure 10). Nutrients which could cause stimulation of algal growth and possibly eutrophication have increased proportionally with waste loads to the Bay. However, no deleterious effects from eutrophication, such as fish kills or algal blooms, are apparent at present in the Bay (Horne and McCormick 1977). Although some industries have come and gone since the 1930's, the major changes in types of waste discharges have been in the treatment of domestic waste.

Domestic, industrial, and agricultural waste all pose potential threats to Dungeness crabs. Many Dungeness crabs spend their entire juvenile existence in the Bay while the remainder of their life cycle is oceanic. Young crabs in the Bay are exposed to the highest concentrations of waste in those areas with poor circulation, particularly during periods of low Delta outflow. Until the 1970's, most wastewater outfalls were not deep water, jet-mixed pipes, but ditches or tide gates from which waste flowed directly into the Bay. At low tide, or on calm days, undiluted waste could be present for several hours before appreciable dispersion.

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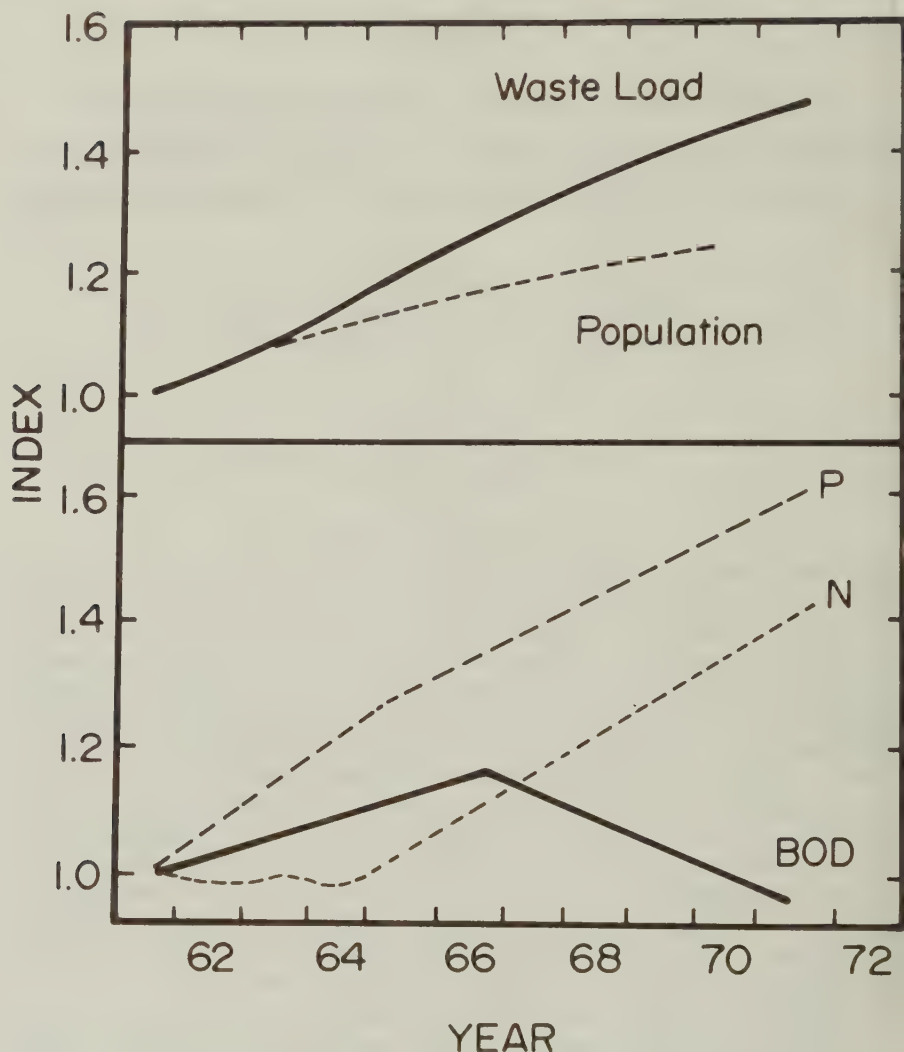


FIGURE 101. Chlorinated waste loads in San Francisco Bay and population growth. N—Nitrogen; P—Phosphorous; BOD—Biological Oxygen Demand. Note decrease in BOD due to improved sewage treatment. Modified from Breslaw (1974).

The main potential toxicants in typical Bay area domestic wastewater are chlorine derivatives, ammonia, surfactants (expressed as methylene blue active substances or MBAS), some soluble organics (such as phenols) and some metals. Industrial waste contains some toxic organics (including petrochemical waste) and metals. Domestic and industrial waste contain varying quantities of substances which increase BOD above the assimilative capacity of the receiving water. Studies on effects of persistent toxic compounds, such as metals, pesticides, and oil-refinery related organics, are discussed in Chapters 18, 19, and 20. This chapter concentrates on effects of chlorine treatment of a typical Bay area

discharge which is comprised of domestic waste with a small proportion of industrial waste. The toxicity of this type of discharge usually persists for only a few days or weeks.

Prior to the mid 1950's, most domestic waste in the Bay was treated at the primary level to remove solids and the remainder was discharged via creeks or ditches. The water contained most nutrients as organic compounds and had a BOD of about 300 mg/liter. In the period 1955 to 1975, two major changes occurred. First, chlorination was used increasingly for disinfection of the treated wastewater prior to disposal. Chlorination was used for all types of domestic waste treatment. Second, more advanced treatment techniques were employed. Secondary treatment changes soluble organic nutrients to inorganic compounds, especially ammonia and phosphate. However, BOD is reduced to about 30 mg/liter. Secondary treatment now dominates waste treatment around the San Francisco Bay-Delta and should be virtually complete by 1985.

Chlorine reacts with ammonia and the organic matter present in sewage to produce four classes of compounds. These are: additions at olefinic bonds, activated ionic substitution, oxidation with reduction of the hypochlorite to chloride, and finally substitution of chlorine for hydrogen on the nitrogen atom of ammonia or an organic amine to produce N-chlorinated compounds. The first three classes are either harmless or produce relatively low concentrations of stable compounds not removed by current dechlorination practices.

The oxidizing agents believed to be the major causes of short-term toxicity in chlorinated waste are the N-chlorinated compounds. These compounds are of two general types, those derived from ammonia and those of organic or carbon-containing amines. These compounds are relatively short-lived, lasting only a few days. They are degraded by organic materials and sunlight, and they react with the bromide ion in seawater to produce possibly more toxic but apparently less stable bromamine compounds.

Since 1975 dechlorination has been used increasingly. This removes at least the acute toxic effects of chlorination in domestic wastewater (Stone et al. 1973). Little information is available on long-term chronic effects of dechlorinated waste.

In recent years, several studies have been conducted at University of California's Sanitary Engineering Research Laboratory (SERL) at the Richmond Field Station on relationships between waste discharges and indigenous organisms, particularly the attached aufwuchs community and fish in the San Francisco Bay-Delta (Krock and Mason 1971; Esvelt et al. 1971; Horne and Kaufman 1974). The bacterial and algal dominated aufwuchs represent lower trophic levels and are highly sensitive to chlorine. These organisms were stimulated by primary and secondary treated, unchlorinated domestic and petrochemical waste, but were greatly inhibited by chlorinated domestic waste. Fish and shellfish represent higher trophic levels. Chlorination of sewage was shown to introduce significant toxicity to fish and was thought to be the largest single source of toxicity entering the Bay. Dechlorination removed this chlorine-induced toxicity. Effects on shellfish were not studied.

The objectives in our study were to compare historical waste chlorination levels in the Bay with San Francisco area crab landings; to conduct bioassays on acute and chronic effects of chlorinated wastes on juvenile Dungeness crabs; and to determine whether there could be any relationship between waste treatment and the long-term decline in the central California crab fishery.

METHODS AND MATERIALS

Historical Wastewater Chlorination in
San Francisco Bay-Delta Waters

The amounts of waste entering the Bay and the degree of chlorination for the period 1950 to 1975 were determined by examination of plant records and conversations with personnel of 25 treatment plants in the San Francisco Bay area and the two major Delta cities of Stockton and Sacramento (Russell and Horne 1977). The 25 Bay area plants represent about 83% of the dry weather flows discharged directly to the San Francisco Bay system. Several major discharges occur in San Pablo and central San Francisco Bay in important nursery areas for Dungeness crabs (Figure 102).

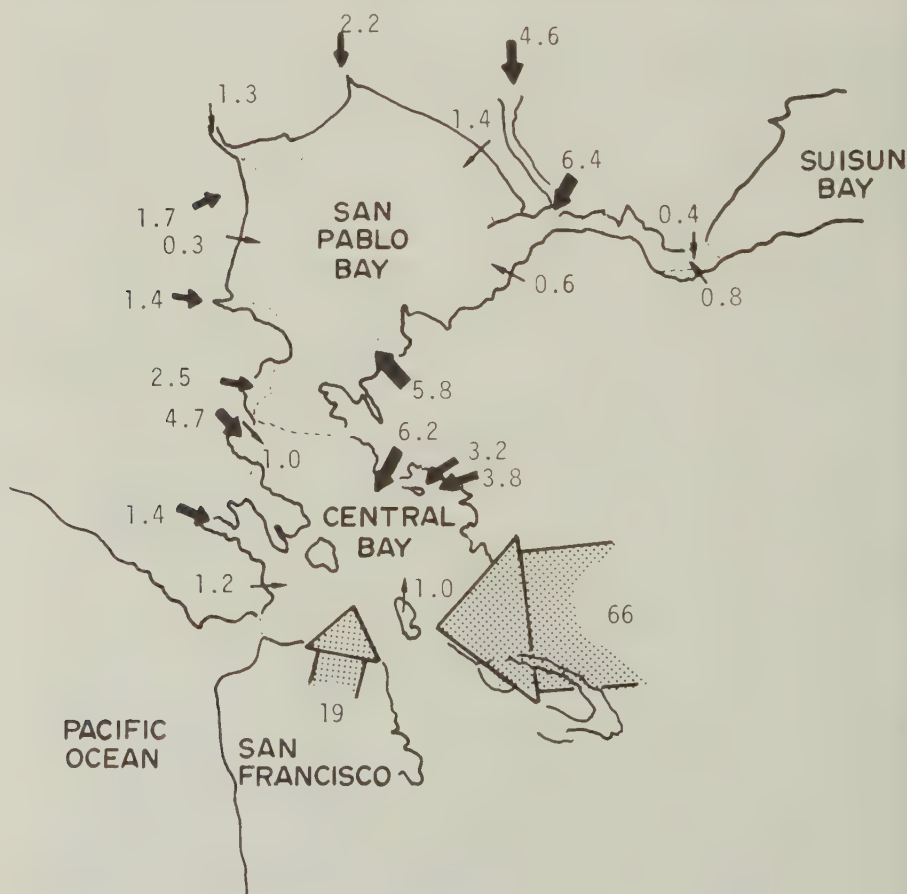


FIGURE 102. Major discharges of chlorinated waste in important nursery areas for juvenile Dungeness crabs. Dotted line indicates nearshore area of little net water flow. Width of arrows and adjacent numbers indicate average waste flows during 1961-1963 in millions of gallons per day. Modified from Pearson et al. (1969)

Russell and Horne (1977) used the actual quantity of chlorine applied, rather than the measured chlorine residual, to determine dry weather flows. The amperometric chlorine residual test most commonly used was often inaccurate, especially in earlier years. Also, many substances interfere with the test. In addition, the residual test will not necessarily detect the C-Cl bond which is often toxic. The increase in chlorine usage in the Bay-Delta area was calculated and compared with the crab decline.

Laboratory Experiments

Laboratory experiments were carried out at SERL during 1978 and 1979. A flow-through, Bay-analog tank system (Figure 103; Valentine et al. 1979; Bennett et al. 1980) supplied with San Francisco Bay water was used to conduct the experiments. To avoid cannibalism, juvenile crabs were held individually in plastic mesh-bottomed cages. Each cage was partially submerged in analog tank water. Each analog tank contained approximately 4 m³ of Bay water pumped from central San Francisco Bay at a station 1000 m offshore from SERL. Many Dungeness crabs spend their entire juvenile existence in central San Francisco and San Pablo Bays (Figures 61–64). Up to 10 separate analog tanks, each with a separate seawater and toxicant supply (Figure 103), were used in our randomized plot-type experiments.

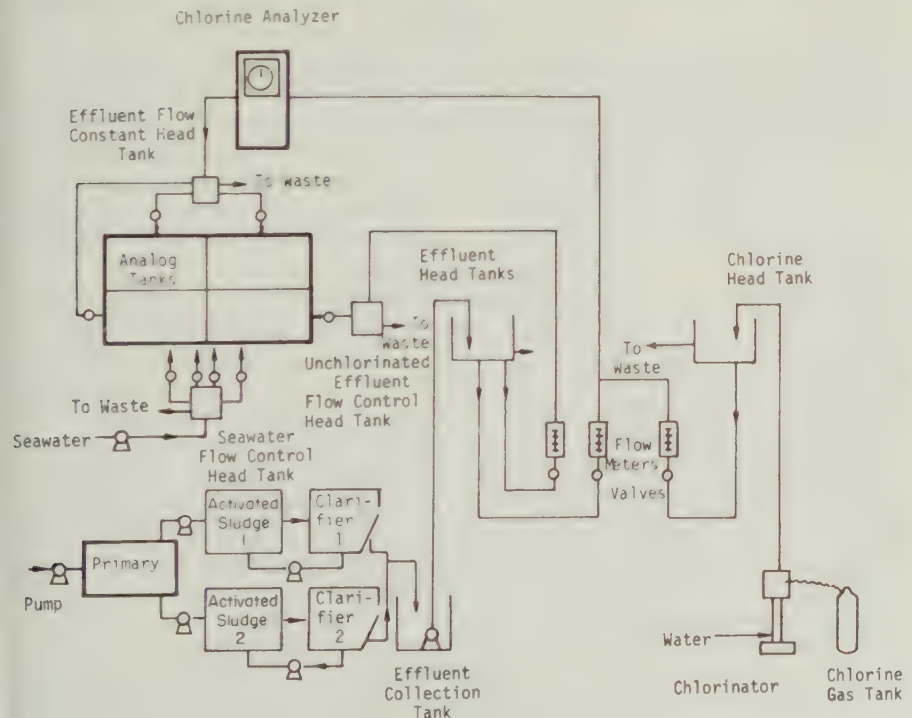


FIGURE 103. Schematic diagram of the analog tank and pilot sewage treatment apparatus.

City of Richmond sewage, a typical Bay Area mixture of mostly domestic with some industrial wastes, was treated to the secondary level at the SERL pilot sewage treatment plant. The wastewater was chlorinated in a system similar to that employed by waste treatment plants in the 1950–1970 period.

In most sewage treatment plants, waste is not discharged immediately after chlorination. It is retained for a time to ensure that all pathogenic bacteria are killed. This residence time partially determines which chlorinated compounds are produced. In our experiments, the residence time between chlorination and dilution was about 30 minutes, a typical full-scale plant time. The waste was then diluted to desired levels with Bay water and pumped to the analog tanks. Complete replacement time for the water in each tank was about 24 hr. Total oxidant residual (TOR), ammonia, pH, temperature, and BOD were monitored frequently in the analog tanks and in the treatment plant. In the first series of experiments, TOR was measured with a Fisher and Porter model 17T/1010 amperometric titrator. In the second series (long-term chronic tests), a more sensitive TOR test, the DPD-Ferrous Titrimetric method (American Public Health Association 1976), was used. With this method we could detect TOR down to 0.006 mg/liter (Bennett et al. 1980).

The most acutely toxic components of the chlorinated waste used were found to be due to the chlorinated residual, mainly amine-type compounds. It was beyond the budget of this project to maintain the pilot sewage treatment plant to produce consistent waste for the longer term chronic tests. Thus, for these experiments a logistically simpler system chlorinating simulated sewage made from ammonia and a peptone broth was used in the analog tanks. The advantage to this approach is that the compounds presumed most toxic, the amines, could be added accurately. A drawback is that any toxicity due to a combination of chronic effects, for example metals and amines, would be lost.

Usually, duplicate treatments with 10 to 30 juvenile crabs per analog tank were used for each level of waste dilution. Deaths were monitored daily and dead crabs removed.

For sub-lethal effects, several types of tests were performed including molting frequency; carapace size; live weight change; and a test developed for this study, the equilibrium recovery time (ERT). ERT is the time taken for crabs to right themselves when turned onto their backs. The equilibrium recovery test is potentially a good measure of long-term ecologically important effects of chlorinated wastes which are known to cause lethargy in fish (A. Venkataramiah, Gulf Breeze Laboratory, Ocean Springs, LA, pers. commun.). The ERT test was carried out using randomized selection and a double blind operator. At times, crabs did not attempt to turn over immediately but would lie absolutely still with limbs out-stretched for several seconds or minutes. This was recorded as a freeze response. ERT's were repeated after freeze responses. Usually, three or four ERT's per crab per test day were obtained.

Two series of experiments were run. The first was a short-term experiment with real waste; the second was a long-term experiment using simulated waste. Size and origin of the crabs used depended on their availability and the starting time of the experiments. For both series of experiments, juvenile crabs were held at the California Department of Fish and Game Marine Culture Laboratory near Monterey prior to transfer to SERL for testing.

In the first series of experiments using real waste, tests were run on juvenile crabs with an average carapace width (excluding 10th anterolateral spines) of

31.5 ± 5.7 mm. These crabs were caught by Department of Fish and Game personnel trawling in Humboldt Bay in northern California where the crab population has not experienced a long-term decline. Acute bioassays were run with chlorinated waste diluted to 5%, 10%, and 50% and a control of 10% unchlorinated waste, all volume for volume dilutions with Bay water. The standard 96-hr (4-day) acute test was extended to 12 days to gather additional data. After 12 days the tests were continued for an additional 11 days without waste to observe for delayed effects of waste discharge. The control was increased to 50% waste during this period to compare with 50% chlorinated waste. Only acute lethal effects and ERT were tested in this experiment.

In the second series of experiments using the simulated waste, tests were run using smaller, younger crabs (average carapace width at beginning was 13.4 ± 1.7 mm) with chlorinated simulated waste diluted to 1% and 10% with Bay water and a control of Bay water only. These crabs were collected as megalopae in the ocean at Drakes Bay (Figure 11) and molted to the first crab instar (about 7 mm) overnight. The experiment was run for 60 days to allow each crab to molt once or twice in the presence of chlorinated waste. It is conceivable that chlorine residual could be most toxic during the molting period. The experiment was continued for an additional 90 days in Bay water only to assess any long-term delayed effects.

RESULTS

Historical review of waste discharge into the San Francisco Bay-Delta revealed that chlorine use was initiated prior to the decline in the Dungeness crab fishery and continued to increase during the decline (Figure 104). Exposure of Dungeness crabs to chlorinated municipal effluent is greatest to juveniles resid-

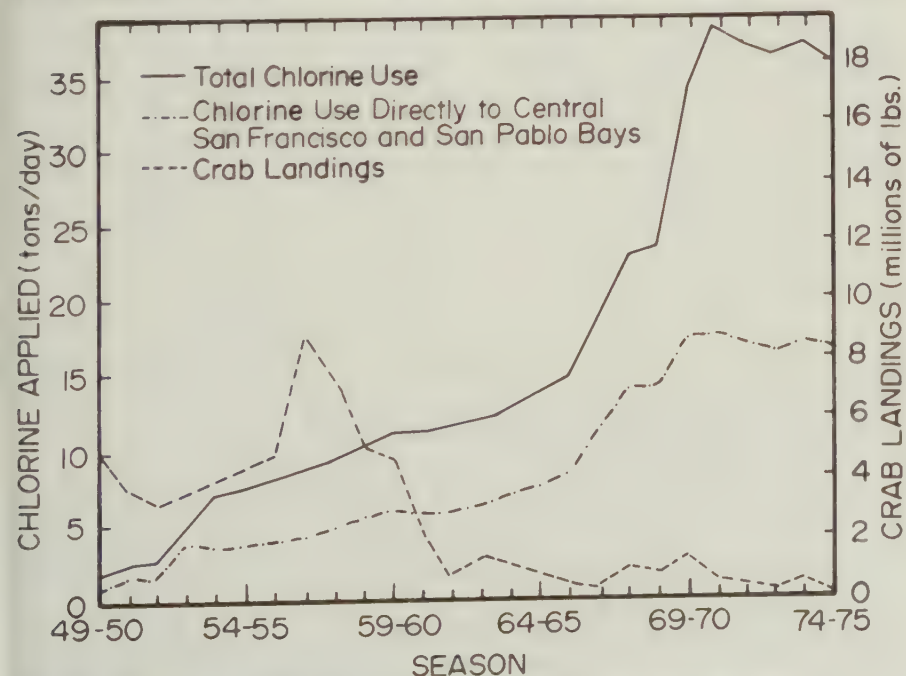


FIGURE 104. Crab landings and chlorine usage in the San Francisco Bay area.

ing in the San Francisco-San Pablo estuary. Any population decrease due to effects on these crabs would be reflected in crab landings as individual year classes reached minimum legal size. Although this does not prove that increased chlorination of wastes caused the failure of the crab population, visual inspection of the data (Figure 104) suggests that a cause and effect relationship could exist.

In our first series of experiments using real sewage, mean TOR levels in 5%, 10%, and 50% chlorinated waste were 0.02, 0.11, and 0.86 mg/liter, respectively. Mortality ranged from zero over 23 days in the control (unchlorinated waste) and 5% chlorinated waste to 100% in 7 days in 50% chlorinated waste (Table 31). The 96 hr LC_{50} was calculated as 0.86 mg/liter TOR. Thus, the extreme toxicity of 50% chlorinated waste contrasts with the low toxicity of the waste itself, even though there was up to 3.5 mg/liter NH_3N at a pH of 7.8 in the control. No mortality occurred in the 10% chlorinated waste over the first 11 days but 35% mortality occurred between days 11–23, although waste flows were discontinued after 12 days. This mortality could be due to a delayed acute effect of TOR.

TABLE 31. Percentage Mortality of Crabs in Chlorinated* and Unchlorinated† Sewage Wastewater.

Experiment day	50% Chlorinated waste (n=10)‡	10% Chlorinated waste (n=20)	5% Chlorinated waste (n=20)	10% & 50% Unchlorinated waste (n=18)
1.....	0.0	0.0	0.0	0.0
2.....	10.0	0.0	0.0	0.0
3.....	20.0	0.0	0.0	0.0
4.....	60.0	0.0	0.0	0.0
5.....	80.0	0.0	0.0	0.0
6.....	90.0	0.0	0.0	0.0
7.....	100.0	0.0	0.0	0.0
8.....		0.0	0.0	0.0
9.....		0.0	0.0	0.0
10.....		0.0	0.0	0.0
11.....		0.0	0.0	0.0
12.....		15.0	0.0	0.0
13.....		20.0	0.0	0.0
14.....		30.0	0.0	0.0
15.....		30.0	0.0	0.0
16.....		30.0	0.0	0.0
17.....		35.0	0.0	0.0
23.....		35.0	0.0	0.0

* After day 12, the chlorinated waste was shut off and Bay water only was used.

† During days 1–12, the unchlorinated waste concentration was 10%; days 13–23, 50%.

‡ n=No. of crabs in experiment.

There was an apparent delay in the ERT response of juvenile crabs exposed to chlorinated waste compared to unchlorinated waste. This delay was more pronounced at the higher level of chlorinated waste (Table 32). The differences between chlorinated and unchlorinated waste were significant ($P \leq 0.05 - 0.01$) in the later days of the experiment.

The second series of experiments was carried out for 150 days with smaller crabs held for 60 days in simulated chlorinated sewage and an additional 90 days in Bay water only. Chlorinated sewage concentrations were 1% and 10% and

TABLE 32. Equilibrium Recovery Time (ERT) and Standard Deviation for Juvenile Crabs Exposed to Two Levels of Total Oxidant Residual (TOR, mg/liter) in Chlorinated Wastewater and a Control of Unchlorinated Wastewater (November 1978).

Experiment day	10% Unchlorinated waste TOR = 0		5% Chlorinated waste TOR = 0.02		10% Chlorinated waste TOR = 0.11	
	ERT * (sec $\pm$ SD)	n †	ERT (sec $\pm$ SD)	n	ERT (sec $\pm$ SD)	n
8.....	1.7 $\pm$ 0.62	9	2.1 $\pm$ 1.34	8	2.5 $\pm$ 1.9	9
10.....	0.9 $\pm$ 0.33	9	1.3 $\pm$ 0.33 ‡	8	2.1 $\pm$ 0.9§	9
12.....	1.0 $\pm$ 0.40	9	1.5 $\pm$ 0.40‡	7	1.8 $\pm$ 0.53§	6

* ERT = Mean of approximately four tests per crab.

† n = Number of crabs tested.

‡ Significantly different from control, $P \leq 0.05$.§ Significantly different from control, $P \leq 0.01$.

the control was Bay water only. Mortality varied between 2 and 8% but could not be ascribed to chlorinated wastes at either level in this experiment. Because the more concentrated chlorinated residuals decayed more rapidly than the more dilute levels, the measured chlorine or TOR residual was approximately 0.033 mg/liter in the 10% wastewater dilution and 0.011 in the 1% dilution (TOR at 10% dilution of real waste in the first experiment was 0.11 mg/liter). Independent variables (other than death) tested against concentration of chlorinated waste were ERT, freeze response, molting frequency, carapace size, and live weight change. Due to the larger sample sizes and more replication, possible interferences due to crab size, age, handling, or sex were analyzed in the analysis of variance used.

The more extensive tests in this series confirmed the earlier ERT results in that chlorinated waste eventually slowed ERT significantly compared to controls (Tables 32 and 33). This effect occurred later with simulated waste than real waste. It is interesting to note that at 60 days, the sexes responded differently

TABLE 33. Equilibrium Recovery Time (ERT) and Standard Deviation for Juvenile Crabs Exposed to a Control of Bay Water and Two Levels of Total Oxidant Residual (TOR, mg/liter) in Simulated Wastewater (Summer-Fall 1979).

Experiment day	Control (Bay water only) TOR = 0		Simulated wastewater			
			1% TOR = 0.011		10% TOR = 0.033	
	ERT * (sec $\pm$ SD)	n †	ERT (sec $\pm$ SD)	n	ERT (sec $\pm$ SD)	n
1.....	1.22 $\pm$ 0.55	30	1.00 $\pm$ 0.44‡	44	1.13 $\pm$ 0.54	45
9.....	0.94 $\pm$ 0.44	30	0.94 $\pm$ 0.33	43	0.90 $\pm$ 0.27	44
22.....	0.91 $\pm$ 0.42	30	1.01 $\pm$ 0.46	45	0.85 $\pm$ 0.30	42
36.....	0.94 $\pm$ 0.34	30	0.98 $\pm$ 0.42	44	1.02 $\pm$ 0.58	44
60.....	0.88 $\pm$ 0.38	26	1.28 $\pm$ 0.54‡	46	1.19 $\pm$ 0.55§	43
Means of days 9-60.....	0.92 $\pm$ 0.39	116	1.06 $\pm$ 0.47‡	178	0.99 $\pm$ 0.46	173

* ERT = Mean of 3 tests per crab.

† n = Number of crabs.

‡ Significantly different from control, $P < 0.05$.§ Significantly different from control, $P < 0.01$.

to chlorinated effluent. Females showed a slightly slower ERT than males ($P \leq 0.05$).

Overall, crabs exposed to chlorinated waste exhibited a significantly greater percentage of freeze responses than the controls (Table 34).

TABLE 34. Percentage of Freeze Responses during ERT Tests of Crabs Exposed to a Control of Bay Water and Two Levels of Total Oxidant Residual (TOR, mg/liter) in Simulated Chlorinated Wastewater (Summer-Fall 1979).

Experiment day	Control (Bay water only) TOR = 0	Simulated wastewater	
		1% TOR = 0.011	10% TOR = 0.033
	%*Showing freeze response	%†Showing freeze response	%†Showing freeze response
1	21	24	29
9	39	31	31
22	14	33	29
36	8	16	29
60	6	29	34
Mean	17.6	26.6	30.4

* % of approximately 90 ERT tests/day (30 crabs $\times$ 3 ERT).

† % of approximately 135 ERT tests/day (45 crabs $\times$ 3 ERT).

No obvious biologically important effect of chlorinated waste was found on molting frequency, carapace size, or live weight irrespective of length of time from the previous molt. Results on carapace size change after 150 days were inconclusive.

DISCUSSION

Many aquatic organisms are highly sensitive to the acute, toxic effects of TOR, but not equally so. Large estuarine and coastal crustaceans appear to be least sensitive and freshwater salmonids are affected at the lowest levels (Jolley 1976; Jolley et al. 1977; Horne and Wilde 1979). Our results confirm this trend because San Francisco Bay juvenile Dungeness crabs had a 96-hr LC_{50} of 0.86 mg/liter TOR, one of the highest measured values for a nonmammalian aquatic organism. Our data (Table 31) show that the chlorine residual was the dominant toxic component of city of Richmond's sewage.

Few studies have been carried out to determine long-term or chronic toxicity of TOR, especially for crabs. In the natural aquatic environment few crabs would ever die of chlorine/bromine poisoning directly because their natural predators would kill and eat them long before this occurred. However, in the highly productive and competitive estuarine environment even a relatively small, deleterious behavioral effect of wastewater could be sufficient to alter the ecological balance against the juvenile crabs. The significance of our findings that very low levels of TOR (0.01 mg/liter) affect the righting response of juvenile crabs in the Bay should be interpreted in the light of possible effects in a competitive shallow-water ecosystem.

Although it is difficult to calculate the exact value of chlorine residual in the areas in which the juvenile crabs grow, a variety of different estimates can be made. Bennett et al. (1980) made calculations of chlorine residuals involving the

volume of water in central, northern, and upper San Francisco Bay, estimated waste or chlorine loadings, estimated hydraulic residence times at high and low Sacramento River flows, and TOR decay kinetics in fresh and saline waters. In areas in which juvenile crabs live there is apparently insufficient dilution to reduce TOR to below the level at which equilibrium behavior is affected. Even if wastes were diluted rapidly throughout the 2 km^3 of the whole north Bay, the critical value ($\sim 0.01 \text{ mg/liter}$) is approached and possibly exceeded depending on the decay kinetics of TOR selected. Critical levels were almost certainly exceeded by a large amount in the shallow, vertically mixed waters along the shoreline where the little-diluted waters of 1955–1970 were discharged.

We know little of the historical, spatial, and depth distribution of juvenile Dungeness crabs in the Bay. However, recent studies (Tasto, Chapter 9) show that juvenile crabs are widely distributed in areas affected by waste water (Figures 61–64). Our laboratory tests indicate that the use of chlorine for wastewater disinfection could have adversely affected survival of juvenile crabs in the Bay. One might speculate that slowed responses would make them more susceptible to predation and thereby may have contributed to the observed decline in catches. If so, then the dechlorination of wastes begun in the mid 1970's, and now almost universal in the Bay, would be expected to be beneficial for crab recovery. This prediction assumes that crab toxicity was due to a narcotizing effect of the N-Cl or N-Br fragment alone and not to C-Cl or C-Br since these are not removed by dechlorination. Also, we assume that there was no synergistic effect between TOR and other toxicants or natural features such as temperature.

We recommend that current dechlorination procedures be continued for those wastes which contain high levels of nitrogenous organic material. In addition, further studies are needed on the role of C-Cl, C-Br, their decay rates, whether there are synergistic reactions with other toxicants known to be in the Bay, and whether these factors influence the observed effects of behavior of juvenile crabs which could reduce their ability to survive in northern San Francisco Bay.

Chapter 18

FIELD AND LABORATORY STUDIES
OF TOXIC TRACE ELEMENTS IN
DUNGENESS CRABS

by

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INTRODUCTION

The decline of the San Francisco Dungeness crab, *Cancer magister*, fishery during the early 1960's (Farley, Chapter 2) was concurrent with a rapid expansion of urbanization and industrialization in the areas surrounding San Francisco Bay. Urban effluent entering the Bay system during the 1961–1964 period included an estimated average daily load of 277 tons of organic suspended solids, 61 tons of oil and grease, and 11 tons of heavy metals (Pearson et al. 1970). In addition, the Bay system for decades has been receiving agricultural runoff from the Sacramento-San Joaquin Valley.

The degree to which toxic trace elements may have been responsible for the decline of the crab population in the San Francisco area and for preventing its recovery has never been ascertained. Because much of the technology used to determine levels of trace elements in biological tissues is relatively new, no historical data exist which document these levels in crab tissues when landings were high. Lacking historical baseline data, the approach used in this study has been to determine current levels of potentially toxic elements in tissues of San Francisco area crabs and compare them to levels of the same elements in tissues of crabs from the Eureka area, where the population appears healthy as evidenced by recent high landings (Farley, Chapter 2). Where statistically significant differences between areas were found in the tissue levels of a particular element, bioassays, in which crabs were exposed to a range of concentrations of that element, were conducted to assess the biological significance of the differences.

Crabs enter the Bay as early-instar juveniles and leave as they approach maturity (Tasto, Chapter 10). An assumption made in this study is that it is during their residence within the Bay system that crabs are exposed to the greatest concentrations of most toxicants (Eaton 1979). Therefore, juvenile crabs were used in the bioassays.

For each element under investigation, two kinds of bioassays were conducted: acute and chronic. Acute bioassays were used to determine the concentration of a toxic element that is lethal to 50% of the crabs (LC_{50}) within 96 hr. This information is useful in evaluating (i) the relative toxicity of various elements to juvenile crabs and (ii) the relative sensitivity of juvenile crabs to a particular element as compared to other organisms which have been similarly tested.

Chronic bioassays were used to assess the effects of sublethal concentrations of toxicants over a longer period (60 days). Using information gained from acute bioassays, concentrations of elements under investigation were used that would result in hepatopancreas tissue levels in test animals at least as high as those

found in crabs from San Francisco Bay. Growth of test animals was monitored and simple behavioral tests were attempted in an effort to uncover anomalies which could be attributed to the element under investigation.

METHODS

Collection and Analysis of Field Samples

The original collection of crabs for tissue analysis was made during January–March 1975. Adult crabs for the San Francisco sample were collected from the Gulf of the Farallones (Figure 11) at depths ranging from 6 to 45 fm by means of traps and trawls operated from commercial fishing vessels. Eureka adults were taken from 15 fm off the Eel River mouth and the south spit of Humboldt Bay by traps fished from the Department's patrol boat BLUEFIN. San Francisco juveniles were captured by ringnets in central San Francisco and San Pablo Bays in 2 to 3 fm. Eureka area juveniles were taken by trawl in about 5 fm from south Humboldt Bay.

San Francisco adult males averaged 150.4 mm in carapace width (cw), females 150.8 mm, and juveniles 84.7 mm. Adult males from Eureka averaged 150.8 mm, females 153.3 mm, and juveniles 82.2 mm (Table 35).

Crabs were frozen soon after capture and kept frozen until tissue excisions could be made. Samples of muscle and hepatopancreas tissues were excised from each crab. Because of the small amount of tissue available in the juveniles, composite samples were made from groups of two to four juvenile crabs. In all, samples were obtained from 25 adult male and 26 adult female crabs from each area; 98 juveniles from San Francisco Bay were represented by 36 composite samples and 100 Humboldt Bay juveniles contributed to 37 composite samples. Each sample was divided and replicates were submitted for analysis to Moss Landing Marine Laboratories (MLML) and to the Department's Water Pollution Control Laboratory (WPCL).

At MLML, levels of cadmium, copper, iron, manganese, silver, and zinc were determined by atomic absorption spectrophotometry. At WPCL, mercury was determined by cold vapor atomic absorption, lead by conventional atomic absorption, and arsenic, barium, bromine, calcium, chromium, cobalt, copper, iron, potassium, manganese, nickel, selenium, strontium, and zinc were analyzed by X-ray fluorescence in cooperation with the California Department of Food and Agriculture Laboratory (DFA).

During 1978 and 1979, small supplemental collections were made to determine changes in tissue levels over time for those elements found to be significantly higher in San Francisco crabs in 1975. Adult crabs were collected from the San Francisco and Eureka fishing grounds (six of each sex from each area), and 10 juveniles were taken from San Francisco Bay in May–June 1978. Fifteen juveniles were collected from Humboldt Bay in June 1979. Adult males from San Francisco averaged 159.6 mm (cw) and females 146.1 mm. Mean size for Eureka males was 159.5 mm, females 154.6 mm. Juveniles from San Francisco Bay averaged 108.0 mm, while those from Humboldt Bay averaged 98.1 mm (Table 35).

Hepatopancreas tissue samples were taken as before except that juvenile samples were from individual crabs rather than composites. Levels of cadmium, silver, and selenium (elements found to be higher in San Francisco crabs in 1975) were determined in these samples; cadmium and silver at MLML and selenium at DFA.

TABLE 35. Mean Carapace Width (mm)*, Standard Deviation, and Sample Size of Dungeness Crabs Collected from San Francisco and Eureka Areas in 1975 and 1978–79.

<i>Year and area</i>	<i>Adult males</i>	<i>Adult females</i>	<i>Juveniles</i>
1975			
San Francisco			
Mean width	150.4	150.8	84.7
SD	4.10	9.31	11.9
n	25	26	98
Eureka			
Mean width	150.8	153.3	82.2
SD	3.80	7.44	11.6
n	25	26	100
1978–79			
San Francisco			
Mean width	159.6	146.1	108.0
SD	11.3	4.01	9.70
n	6	5	10
Eureka			
Mean width	159.5	154.6	98.1
SD	39.9	4.39	8.74
n	5	5	15

* Excluding 10th anterolateral spines.

Bioassays

Juvenile crabs used in bioassays were collected as early instars in Drake's Bay and Humboldt Bay and transported to the Department's Marine Culture Laboratory (MCL) near Monterey. There they were maintained in individual compartments in flowing seawater and fed chopped squid two or three times per week.

Bioassays were conducted with cadmium, silver, and selenium in seawater. All bioassays were performed at the Department's Marine Bioassay Laboratory (MBL), located adjacent to the MCL. Levels of several trace elements (including cadmium) in the seawater at this laboratory have been shown to be less than one part per trillion (Michael Lorne, Calif. Dep. Fish and Game, unpublished manuscript; Martin et al. 1981). These same studies found no suitable methods for measuring the ambient seawater levels of silver or selenium.

Acute bioassays were preceded by small-scale, static range-finding bioassays which were conducted for a 96-hr period with four crabs at each of four toxicant concentrations covering a thousand-fold range. Four crabs in seawater served as controls. All solutions were aerated and were replaced daily. Exposure chambers were bathed by flowing seawater at ambient temperature.

For the acute (96-hr) and chronic (60-day) bioassays, a proportional diluter modified after Mount and Brungs (1967) was used to deliver predetermined concentrations of toxicants in seawater to the exposure chambers. Duplicate exposure chambers were used for each of five concentrations and for the seawater controls. Each of the 12 exposure chambers contained 10 crabs in individual compartments. The flow rate into each chamber was about 4.5 liters/hr. Seawater was filtered to 10 μ m and supplied at ambient temperature. Toxicant concentrations were monitored periodically during the bioassays.

Crabs were not fed during the range-finding nor acute bioassays. Those used in chronic bioassays were fed diced squid twice per week and uneaten food was

removed the day following feeding. Exposure chambers were cleaned periodically, as needed, by flushing with running seawater.

A crab was judged to be dead if it failed to respond to a stroking of its carapace with a glass rod. Determination of LC_{50} was accomplished by graphical interpolation (American Public Health Association 1976).

Following chronic bioassays, crabs from the highest concentrations were matched against controls in two behavioral tests. In the first, crabs were inverted and the time necessary to right themselves was recorded. In the second test, an unfed crab was placed at one end of a tray downstream from a piece of squid at the opposite end. The time taken to find the food was recorded.

Hepatopancreas tissues from crabs used in the cadmium and silver bioassays were submitted to MLML for toxicant level determination. Selenium levels were determined by DFA.

RESULTS

Toxicant Levels in Field Samples

In all 1975 samples, tissue concentrations of the following elements were below detection limits: lead (detection limit 1.0 ppm), chromium (4.0 ppm), cobalt (4.0 ppm), and barium (150 ppm). In general, tissue concentrations were higher in adult animals (exceptions were manganese and strontium) and higher in hepatopancreas than in the muscle (exceptions were arsenic, potassium, and zinc). Concentrations of most elements were somewhat higher in San Francisco crabs. Highest concentrations of most elements were found in the hepatopancreas of adult females, the oldest crabs as inferred by size in the 1975 samples (After maturity, females grow more slowly than males, and are older than males of equal size [Butler 1961].)

The greatest differences in tissue burdens of potentially toxic elements between the San Francisco and Eureka areas in 1975 were found in levels of cadmium, silver, and selenium in adult female hepatopancreas (Table 36). Cadmium averaged 76.9 ppm in San Francisco females as opposed to 27.2 ppm for Eureka females. Mean concentrations of silver were 24.0 ppm in San Francisco crabs, 10.4 ppm in Eureka crabs. Selenium averaged 9.8 ppm for San Francisco versus 2.9 ppm for Eureka. The differences in means between these two areas were highly significant ($P < 0.001$; Student's *t*-test) for all three elements. Similar differences were found in levels of these elements in adult males and, for silver and selenium, in juveniles.

The small supplemental collection made in 1978 showed a very different picture. Tissue levels of all three elements (cadmium, silver, and selenium) in San Francisco adult females were dramatically lower than the 1975 levels, and were no longer significantly different from levels found in Eureka females (Table 36). Adult male crabs collected in 1978 were larger and presumably older than those in the 1975 collection; therefore, comparison of tissue levels between years would not be meaningful. However, there were no significant differences between San Francisco and Eureka males in 1978 in these three elements.

Juvenile crabs collected in San Francisco Bay in 1978 showed no significant change from the 1975 samples in cadmium or selenium levels, but the mean silver level was higher (8.2 ppm compared to 3.2 ppm; $P < 0.02$) (Table 36). Humboldt Bay juveniles collected in 1979 showed significant drops in levels of cadmium and silver, but a significant increase in selenium levels from 1.4 ppm to 2.4 ppm ($P < 0.01$).

TABLE 36. Mean Levels (ppm) $\pm$ Standard Deviation of Cadmium, Silver, and Selenium in Hepatopancreas Tissue of Dungeness Crabs Collected from San Francisco and Eureka Areas in 1975 and 1978-79.

Area	Adult females					
	Cadmium		Silver		Selenium	
	1975	1978	1975	1978	1975	1978
San Francisco	76.9 $\pm$ 49.8 n = 25	24.2 $\pm$ 8.6 n = 5	24.0 $\pm$ 13.3 n = 24	6.4 $\pm$ 2.3 n = 5	9.8 $\pm$ 5.8 n = 22	4.5 $\pm$ 1.4 n = 5
Eureka	27.2 $\pm$ 21.5 n = 25	21.0 $\pm$ 6.7 n = 4	10.4 $\pm$ 5.6 n = 25	8.4 $\pm$ 2.2 n = 4	2.9 $\pm$ 1.5 n = 22	5.8 $\pm$ 1.7 n = 5
	Adult males					
	Cadmium		Silver		Selenium	
	1975	1978	1975	1978	1975	1978
San Francisco	15.0 $\pm$ 9.4 n = 24	23.1 $\pm$ 10.1 n = 6	5.1 $\pm$ 2.6 n = 24	12.0 $\pm$ 6.8 n = 6	2.0 $\pm$ 1.0 n = 22	5.9 $\pm$ 2.3 n = 6
Eureka	5.8 $\pm$ 5.3 n = 25	38.8 $\pm$ 31.8 n = 5	1.4 $\pm$ 1.4 n = 25	14.7 $\pm$ 9.0 n = 5	1.2 $\pm$ 1.0 n = 25	3.6 $\pm$ 1.0 n = 5
	Juveniles					
	Cadmium		Silver		Selenium	
	1975	1978-79*	1975	1978-79*	1975	1978-79*
San Francisco	3.5 $\pm$ 1.0 n = 36	3.0 $\pm$ 2.6 n = 10	3.2 $\pm$ 1.4 n = 36	8.2 $\pm$ 5.2 n = 10	3.3 $\pm$ 1.3 n = 31	3.6 $\pm$ 3.3 n = 8
Eureka	3.5 $\pm$ 1.3 n = 37	1.2 $\pm$ 0.5 n = 10	1.8 $\pm$ 1.0 n = 37	0.2 $\pm$ 0.1 n = 10	1.4 $\pm$ 1.0 n = 30	2.4 $\pm$ 0.9 n = 15

* Juveniles were collected from San Francisco Bay in 1978 and from Humboldt Bay in 1979.

Bioassays

Cadmium

The acute cadmium bioassay was run with concentrations from 3.1 to 30.0 mg/liter of cadmium (as CdCl_2) in seawater. The number of crabs surviving 96 hr at each concentration was:

Control	20
3.1 mg/liter	19
5.2 mg/liter	12
9.8 mg/liter	7
15.8 mg/liter	1
30.0 mg/liter	0

The 96-hr LC_{50} of cadmium in seawater for juvenile Dungeness crabs is 6.8 mg/liter.

Levels of cadmium in hepatopancreas tissues of crabs from this bioassay show that crabs are capable of concentrating large quantities of cadmium in the hepatopancreas within a short time (over 20 times the concentration in seawater within 24 hr) (Table 37). In general, cadmium concentrations in tissues showed

TABLE 37. Mean Levels (ppm) $\pm$ Standard Deviation of Cadmium in Hepatopancreas of Dungeness Crabs from 96-hr Bioassay.

	Concentration of Cd in test solution (mg/liter)					
	Controls	3.1	5.2	9.8	15.8	30.0
Dead at 24 hr						647.4 $\pm$ 194.5 n = 5
Dead at 48 hr				599.0 n = 1	787.8 $\pm$ 135.9 n = 5	862.8 $\pm$ 245.3 n = 5
Dead at 72 hr			517.5 $\pm$ 162.0 n = 2	956.2 $\pm$ 240.0 n = 5	556.7 $\pm$ 134.4 n = 2	1029.7 $\pm$ 260.0 n = 4
Dead at 96 hr		548.5 n = 1	573.1 $\pm$ 42.8 n = 5	796.4 $\pm$ 278.4 n = 2	850.1 $\pm$ 125.1 n = 4	
Alive at 96 hr		177.1 $\pm$ 87.0 n = 4	257.0 $\pm$ 97.8 n = 4	349.8 $\pm$ 222.6 n = 3	798.5 n = 1	
Alive 96 hr in Cd + 72 hr in seawater ..	4.1 $\pm$ 2.0 n = 10	294.8 $\pm$ 174.3 n = 7	378.8 $\pm$ 146.2 n = 4	274.9 n = 1		

a direct correlation with concentrations in test solutions and with time of exposure. Most of the crabs that died during the bioassay had hepatopancreas cadmium levels in excess of 500 ppm (the highest was 1363 ppm), while most of the survivors had levels below 400 ppm. (The highest hepatopancreas cadmium level we have found in nature was 241 ppm from an adult female crab from the Gulf of the Farallones taken in 1975.) Cadmium levels in hepatopancreas tissue of control crabs averaged 4.1 ppm.

Most of the crabs held in cadmium-free seawater for 72 hr after the bioassay had higher cadmium levels in their hepatopancreas tissue than did those sacrificed upon completion of the bioassay. This suggests that cadmium in other parts of the body may move to the hepatopancreas and accumulate in that organ.

In the 60-day bioassay to determine effects of chronic exposure to sublethal concentrations of cadmium on juvenile crabs, exposures ranged from 0.030 to 0.35 mg/liter. There were no statistically significant differences in rate of growth nor of molting among crabs at these concentrations. Behavioral tests of righting and food-finding abilities were inconclusive. Nearly all crabs, whatever their history of cadmium exposure, righted themselves immediately, often before the stop-watch could be started. In the food-finding test, none of the crabs, though unfed for periods of up to 8 days, showed any attempt to search for the squid during a 3-hr test. This is in contrast to the often eager acceptance of squid by these same crabs during the bioassay. By subjective appraisal, there was no obvious loss of vigor by crabs exposed to cadmium at the concentrations used in this bioassay.

Levels of cadmium in hepatopancreas tissues averaged about 2000 times the concentrations to which the crabs were exposed (Table 38). Tissue levels from the lowest of these concentrations (0.030 mg/liter) approximated those found in adult female crabs from the Gulf of the Farallones in the 1975 collections (average 76.9 ppm).

TABLE 38. Levels of Cadmium in Hepatopancreas of Dungeness Crabs from 60-Day Bioassay.

<i>Concentration of Cd in seawater</i>	<i>Concentration of Cd in hepatopancreas</i>		
	<i>Mean (ppm)</i>	<i>Standard deviation</i>	<i>n</i>
Control	6.14	4.12	10
0.030 mg/liter	60.8	17.2	10
0.056 mg/liter	103.0	33.0	10
0.12 mg/liter	249.8	47.7	9
0.20 mg/liter	346.7	104.1	10
0.35 mg/liter	705.6	278.6	10

Silver

Concentrations of silver (as AgNO_3) in seawater in the acute bioassay ranged from 0.10 to 1.80 mg/liter. The number of surviving crabs at each concentration at 96 hr was:

Control	20
0.10 mg/liter	15
0.31 mg/liter	6
0.51 mg/liter	4
0.90 mg/liter	3
1.80 mg/liter	0

The 96-hr LC_{50} of silver in seawater for juvenile Dungeness crabs is 0.19 mg/liter.

Levels of silver in hepatopancreas tissues of crabs from this bioassay correlated roughly with concentrations in test solutions and with time of exposure (Table 39). In contrast with the acute cadmium bioassays, several mortalities occurred at relatively low concentrations and short exposures. Silver concentrations in the hepatopancreas of these crabs were also relatively low, suggesting that at these exposures silver is lethal to crabs before it can be accumulated appreciably in the hepatopancreas. (The highest hepatopancreas silver level we have found in nature was 49.9 ppm from an adult female crab taken in the Gulf of the Farallones in 1975.) Control crabs in the bioassay averaged 1.50 ppm of silver in hepatopancreas tissues.

Silver concentrations in seawater in the chronic bioassay ranged from 0.0019 to 0.0186 mg/liter. During the 60-day period of this bioassay, considerable mortality occurred among both the control crabs and those at low silver concentrations. The number of crabs that died at each concentration was:

Control.....	6
0.0019 mg/liter	7
0.0047 mg/liter	4
0.0070 mg/liter	4
0.0119 mg/liter	1
0.0186 mg/liter	1

Although causes of death were not determined, the inverse relation of mortality to silver concentration make it unlikely that silver was a contributing factor. Behavioral tests similar to those for the cadmium bioassay were equally inconclusive. No sublethal effects on growth or vigor due to silver were apparent.

Levels of silver in hepatopancreas tissues of crabs from this bioassay were directly related to concentrations of silver in test solutions with a concentration factor of about 1000 times (Table 40). These levels exceeded those found in any of the field samples of juvenile crabs but did not reach those of adult female crabs in the 1975 samples from the Gulf of the Farallones (average 24.0 ppm)

Selenium

In the acute selenium bioassay, concentrations (as SeO_2) in seawater ranged from 3.85 to 40.65 mg/liter. The number of crabs surviving 96 hr at each concentration was:

Control.....	20
3.85 mg/liter	20
8.55 mg/liter	19
13.75 mg/liter	15
22.45 mg/liter	8
40.65 mg/liter	1

The 96-hr LC_{50} of selenium in seawater for juvenile Dungeness crabs is 19.5 mg/liter.

TABLE 39. Means Levels (ppm) $\pm$ Standard Deviation of Silver in Hepatopancreas of Dungeness Crabs from 96-hr Bioassay.

	Concentration of Ag in test solution (mg/liter)					
	Controls	0.10	0.31	0.51	0.90	1.80
Dead at 24 hr.....		2.62 $\pm$ 2.37 n = 2	8.88 n = 1	6.20 $\pm$ 3.15 n = 3	3.99 n = 1	14.3 $\pm$ 4.5 n = 3
Dead at 48 hr.....		2.57 n = 1	12.8 $\pm$ 5.4 n = 3	26.0 $\pm$ 17.8 n = 3	37.3 $\pm$ 40.6 n = 3	63.4 $\pm$ 59.8 n = 3
Dead at 72 hr.....		12.0 n = 1	29.6 $\pm$ 12.1 n = 3		15.6 $\pm$ 3.8 n = 2	68.4 $\pm$ 41.1 n = 3
Dead at 96 hr.....		19.8 n = 1	68.4 $\pm$ 28.4 n = 3	198.4 $\pm$ 71.0 n = 2	43.4 n = 1	136.7 $\pm$ 173.0 n = 3
Alive at 96 hr.....		18.5 $\pm$ 8.9 n = 3	41.3 $\pm$ 16.4 n = 3	62.9 $\pm$ 50.3 n = 2	59.2 $\pm$ 41.0 n = 2	
Alive at 96 hr in Ag + 72 in seawater.....	1.50 $\pm$ 0.53 n = 10	26.5 $\pm$ 10.3 n = 3	203.8 $\pm$ 98.7 n = 2	141.5 $\pm$ 4.8 n = 2	36.4 n = 1	

TABLE 40. Levels of Silver in Hepatopancreas of Dungeness Crabs from 60-day Bioassay.

Concentration of Ag in seawater	Concentration of Ag in hepatopancreas		
	Mean (ppm)	Standard deviation	n
Control	1.46	0.86	13
0.0019 mg/liter	2.50	1.40	11
0.0047 mg/liter	4.32	2.18	9
0.0070 mg/liter	5.83	2.20	10
0.0119 mg/liter	11.2	7.85	10
0.0186 mg/liter	16.1	7.44	12

As in the other acute bioassays, there was a rough correlation of toxicant levels in the hepatopancreas tissue with concentration of test solutions and with time of exposure (Table 41).

The chronic selenium bioassay was run with concentrations ranging from 0.33 to 3.33 mg/liter. This bioassay was beset with weather related difficulties. Twelve days after the beginning of the experiment, a wind storm caused interruptions of electrical service and seawater supply to the laboratory, lasting for 30 hr on one occasion and 12 to 18 hr at another. Later, heavy rains filled the toxic waste receiving pond at MBL causing the bioassays to be terminated at 34 days. As a consequence of electrical and seawater interruptions, test animals were subjected to increased temperature variations, decreased oxygen, and increased concentrations of metabolic waste products resulting in considerable mortality. Crabs in the highest selenium concentrations were the most affected. The number of mortalities at each concentration was:

Control	1
0.33 mg/liter	4
0.59 mg/liter	13
1.06 mg/liter	11
1.85 mg/liter	13
3.33 mg/liter	18

Thus, selenium concentrations thought to be sublethal under "normal" conditions became lethal when combined with other environmental stresses.

Levels of selenium in hepatopancreas tissues of crabs from this bioassay were related to concentrations of test solutions (Table 42). The concentration factor for selenium ($< 100x$) was considerably lower than were those for cadmium ($\sim 2000x$) or silver ($\sim 1000x$).

Results of this bioassay show that the presence of high concentrations of selenium may cause mortalities among crabs subjected to environmental stresses that they might otherwise survive. Yet, selenium levels that were lethal in this bioassay were much higher than those to which San Francisco Bay juvenile crabs are subjected. (The highest hepatopancreas level of selenium in a juvenile crab from the field collection is 8.8 ppm in a large [115 mm cw] juvenile taken in San Francisco Bay in 1978.)

TABLE 41. Mean Levels (ppm) $\pm$ Standard Deviation of Selenium in Hepatopancreas of Dungeness Crabs from 96-hr Bioassay.

	Concentrations of Se in test solution (mg/liter)				
	Control	3.85	8.55	13.75	22.45
Dead at 24 hr					40.65
					102.7 $\pm$ 19.3 n = 5
Dead at 48 hr					72.6 $\pm$ 26.3 n = 5
					101.4 $\pm$ 46.4 n = 8
Dead at 72 hr			76.1 n = 1	20.0 $\pm$ 2.3 n = 2	81.5 $\pm$ 45.4 n = 5
				66.6 $\pm$ 64.3 n = 3	54.7 $\pm$ 21.3 n = 4
Dead at 96 hr					95.3 $\pm$ 32.5 n = 2
					58.3 $\pm$ 25.4* n = 3
Alive at 96 hr	1.8 $\pm$ 0.7 n = 4	17.9 $\pm$ 10.7 n = 4	23.5 $\pm$ 11.7 n = 5	37.8 $\pm$ 23.4 n = 8	56.1 $\pm$ 33.9 n = 8
					see above

* One of these crabs survived 96 hr but, because of a mix-up in labels, could not be identified.

TABLE 42. Levels of Selenium in Hepatopancreas of Dungeness Crabs from 60-day Bioassay.

<i>Concentration of Se in seawater</i>	<i>Concentration of Se in hepatopancreas</i>		
	<i>Mean (ppm)</i>	<i>Standard deviation</i>	<i>n</i>
Control	1.7	0.9	10
0.33 mg/liter	15.0	4.4	16
0.59 mg/liter	22.4	15.5	7
1.06 mg/liter	38.7	15.3	9
1.85 mg/liter	64.8	43.9	7
3.33 mg/liter	220.3	66.3	2

DISCUSSION

As the San Francisco Bay system is the nursery area for a major portion of the central California crab population (Tasto, Chapter 10), it is axiomatic that a healthy population is dependent upon water quality within the Bay system. Among those agents which may be compromising local water quality and detrimental to crabs, this study has focused upon three elements deemed to be the most likely suspects owing to differences found in tissue burdens between San Francisco and Eureka crabs in the 1975 samples. The differences in tissue burdens between the 1975 samples and those taken in 1978 and 1979 may be an expression of year-to-year variability in toxicant concentrations of the waters inhabited by the crab, or they may reflect a long-term decrease in the amount of toxicants entering the Bay system.

This study was not designed to explore possible synergistic effects of combinations of elements, nor possible synergisms with other toxicants or with unfavorable natural environmental factors (e.g. temperature, salinity, or oxygen concentration). However, the juvenile crab is motile and may avoid those unfavorable environmental conditions it is able to detect.

The problem of determining effects of sub-lethal concentrations of toxicants was not resolved in this study. The 60-day chronic bioassays were too short to reveal subtle differences in growth rates, and the behavioral tests attempted were inconclusive. The value of subjective assessments of vigor or of "well-being" which cannot be quantified is limited.

In the laboratory, tissue levels of crabs exposed to the three elements studied were shown to be related to the experimental environmental concentrations of those elements. By inference, tissue levels of these elements currently found in San Francisco area crabs are indicative of environmental concentrations lower than those that have been demonstrated to be harmful in these bioassays. Within the limitations cited, this study found no evidence that environmental levels of cadmium, silver, and selenium in San Francisco Bay, when tested singly under conditions optimal for crabs, prevent the recovery of the San Francisco crab population. Effects of synergism among toxicants or with adverse environmental factors deserve further investigation.

Chapter 19

CHLORINATED HYDROCARBON PESTICIDES AND POLYCHLORINATED BIPHENYLS IN DUNGENESS CRABS

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INTRODUCTION

In the decades preceding the collapse of the San Francisco Dungeness crab, *Cancer magister*, fishery, chlorinated hydrocarbon pesticides (of which DDT was the most prominent) and polychlorinated biphenyls (PCB's) were in increasingly widespread use throughout the world. These compounds are notably persistent in the environment, accumulate in tissues of organisms, and have been shown to interfere with calcium metabolism in vertebrates and to be toxic to many aquatic organisms (Nicholson 1967; Risebrough et al. 1968; Peakall and Lincer 1970; Walker 1976). Because of these adverse environmental consequences, use of many of these compounds has been banned or severely restricted in the United States since the early 1970's.

A study of chlorinated hydrocarbon pesticides and PCB's in Dungeness crab tissues was undertaken as a part of studies of the role of environmental toxicants in the decline of the San Francisco area crab population (Horne et al., Chapter 17; Haugen, Chapter 18; Guard et al., Chapter 20). Tissue levels of pesticides and PCB's in San Francisco area crabs reported by earlier investigators were compared to current levels to determine changes in body burden over time. Comparisons were also made between current tissue levels in San Francisco crabs and levels in crabs from the Eureka area where continued high landings are indicative of a healthy population. Findings of current high levels in San Francisco crabs relative to those found in earlier studies or to current levels in Eureka would indicate where further investigations (e.g. bioassays) might be warranted.

Earlier workers reporting on levels of DDT and its metabolites in crabs from the San Francisco area include Modin (1961), Willis (1970), and Earnest and Benville (1971). Results of these investigations are difficult to compare because of differences in sample size, age of animals sampled, or tissues tested, and because of increasing sophistication of analytic techniques.

In general, these earlier workers found total DDT residues (including DDT, DDD, and DDE) in samples of muscle tissue (flesh) or in whole crabs from San Francisco Bay which ranged from about 0.02 to 0.25 ppm. Samples of flesh or of whole crabs taken from outside the Bay ranged from about 0.01 to 0.14 ppm. Crab eggs ranged from about 0.05 to 0.4 ppm. Samples of hepatopancreas ranged from 1.3 to 4.3 ppm total DDT residues.

PCB's have been found in Dungeness crab flesh (0.006–0.06 ppm; eight crabs) and eggs (0.11 ppm; one sample) taken from the San Francisco area in December 1973 (James Rote, Hopkins Marine Station, pers. commun.). McDermott et

al. (1975) reported PCB concentrations ranging from 0.09 to 4.9 ppm in the muscle tissue of yellow crabs, *Cancer anthonyi*, collected in southern California in 1971 and 1972. Gonad concentrations of PCB's in these same yellow crab samples ranged from 0.57 to 29 ppm. Duke et al. (1970) reported PCB levels ranging from 1.0 to 7.0 ppm in composite whole-body samples of blue crabs, *Callinectes sapidus*, collected from Escambia Bay, Florida in 1969. In a sublethal bioassay, these workers exposed juvenile blue crabs to concentrations of 3.5 to 4.2 ppb of the PCB Aroclor 1254 in seawater for a 20-day period. At the conclusion of the bioassay, whole-body concentrations averaged 23 ppm PCB. Four weeks following exposure, a sample of these crabs averaged 11 ppm.

METHODS

During winter 1973-74, samples of ovigerous female Dungeness crabs were collected from San Francisco (Gulf of the Farallones; Figure 11) and Eureka (Figure 18) areas for pesticide and PCB analysis. The crabs were frozen soon after collection and shipped to the Department of Fish and Game Pesticide Laboratory, Sacramento for dissection and analysis. Muscle tissue and (or) eggs from 13 San Francisco and five Eureka crabs were analyzed. The crabs ranged in carapace width (CW, excluding 10th anterolateral spines) from 135 to 164 mm (San Francisco area) and 132 to 164 mm (Eureka area).

Collections of juvenile crabs were made in San Francisco-San Pablo Bays in January, March, April, and September 1975. Eureka area crabs were collected from Humboldt Bay in May 1975. In all, 105 crabs ranging from 58 to 100 mm CW from San Francisco Bay and 102 crabs ranging from 54 to 98mm CW from Humboldt Bay were used. Crabs were frozen shortly after capture and transported to the Department of Fish and Game Laboratory at Monterey. Samples of muscle and hepatopancreas tissue were dissected from each crab and composite samples prepared. Each composite consisted of tissue of from 1 to 10 crabs depending on the amount of tissue available from each crab. Composite samples were submitted to the Department's Pesticide Laboratory for analyses.

Tissue levels of chlorinated hydrocarbon pesticides and PCB's were determined by gas chromatography at the Pesticide Laboratory.

RESULTS AND DISCUSSION

The only chlorinated pesticide residue found in all crab tissues analyzed was DDE.

Levels of DDE in muscle tissue from adult females averaged 0.02 (0.017 SD) and 0.01 (0.003 SD) ppm from San Francisco and Eureka areas, respectively. DDE levels in eggs averaged 0.06 (0.03 SD) and 0.02 (0.01 SD) ppm, respectively. Between area differences were not significant ($P > 0.05$). All levels were within or (for Eureka crab eggs) lower than ranges reported from earlier studies. Because these levels were quite low and between area differences were not significant, no further analyses of adults were made. PCB's were not identified at the laboratory's detection limit (0.005 ppm). However, PCB's have been found in San Francisco area adult crabs (as indicated earlier) in analyses at Hopkins Marine Station (James Rote, pers. commun.).

Levels of DDE in both muscle and hepatopancreas of San Francisco Bay juvenile crabs were lower than in Humboldt Bay juveniles (Table 43), although

TABLE 43. Levels* of DDE and PCB's in Juvenile Dungeness Crab Tissues from Humboldt Bay and San Francisco-San Pablo Bay.

Location	Tissue	No crabs	Composite samples	DDE (ppm)		PCB's † (ppm)	
				Mean	SD	Mean	SD
Humboldt Bay	muscle	102	16	0.007	0.006	0.013	0.004
	hepato-pancreas	102	14	0.15	0.074	0.35	0.18
San Francisco-San Pablo Bay	muscle	105	20	0.004	0.004	0.032	0.020
	hepato-pancreas	105	20	0.091	0.12	0.92	0.45

* Wet weight

† PCB's—Total of Aroclors 1248 + 1254 + 1260

the between-area differences were not statistically significant ($P > 0.05$). Eureka crabs averaged 0.007 ppm DDE in muscle tissue and 0.15 ppm in hepatopancreas tissue. Corresponding levels in San Francisco crabs were 0.004 ppm and 0.09 ppm, respectively. In contrast, levels of PCB residues (reported as totals of Aroclors 1248, 1254, and 1260) in San Francisco crabs (muscle 0.032 ppm, hepatopancreas 0.92 ppm) were significantly higher ($P < 0.01$) than those found in Eureka crabs (muscle 0.013 ppm, hepatopancreas 0.35 ppm).

The levels of DDE in San Francisco area juvenile crabs reported here are lower than those found in crab tissues in earlier studies. PCB levels, while higher in San Francisco than in Eureka crabs, are similar to those reported by Rote from his 1973 collection and lower than those reported in yellow crabs from southern California (McDermott et al. 1975) and blue crabs from Florida (Duke et al. 1970). From the low residue levels found in this study, it seems unlikely that chlorinated hydrocarbon pesticides or PCB's are responsible for preventing the recovery of the San Francisco area Dungeness crab population. However, despite the low residues found and the increasingly stringent controls on uses of these substances, it is still uncertain whether these compounds are having any other influence on the crab population.

Chapter 20

HYDROCARBONS IN DUNGENESS CRABS, *CANCER MAGISTER*, AND ESTUARINE SEDIMENTS

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INTRODUCTION

Among the many possible causes for the long-term decline in the Dungeness Crab fishery in central California (Figure 10), we were most interested in petroleum hydrocarbon pollutants in crabs within the San Francisco Bay estuarine system. Many Dungeness crabs utilize San Francisco and San Pablo Bays as nursery areas during their juvenile stage (Tasto, Chapter 10) while the remainder of their life cycle and the fishery occur in the ocean.

Pearson et al. (1970) estimated that chronic inputs of oil and grease to the Bay system from 1961 to 1964 averaged 61 tons per day from various sources. Storrs et al. (1964), DiSalvo and Guard (1975), and numerous measurements made by the Environmental Protection Agency and Army Corps of Engineers have demonstrated the presence of high levels of hydrocarbons ($> 10^3$ ppm, dry wt basis) in San Francisco Bay system sediments.

DiSalvo and Guard (1975) demonstrated that sediment hydrocarbons in the Bay system are derived from suspended sediments. Suspended matter is conserved in the Bay by sedimentation primarily in shoal regions of east Bay and the shallows of San Pablo Bay (Selleck and Pearson 1960), a pattern consistent with data from Bay current studies (Conomos et al. 1971).

The term "petroleum hydrocarbons" includes a varied array of aromatic and aliphatic compounds, a number of which are known to be toxic to marine invertebrates (Hyland and Schneider 1976). Several of the aliphatic or saturated hydrocarbons found in petroleum are also produced by marine organisms, primarily phytoplankton. Hydrocarbons from Oakland Middle Harbor sediments have been found to contain an overwhelming percentage of fossil hydrocarbons, as opposed to those of recent biogenic origin, with the general characteristics of residual fuel and lubricating oil (U.C. Berkeley's Naval Biosciences Laboratory, unpublished data). Also present is a diverse suite of polynuclear aromatic hydrocarbons (PAH) which include some of the most toxic petroleum hydrocarbons. Exposure of juvenile crabs to these pollutant hydrocarbons presumably could result in either acute or sublethal effects which would be reflected in population dynamics.

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Accumulation of pollutant hydrocarbons in the tissues of any marine organism is one criterion for exposure and is often the simplest to assess. The goal of our study, in part, was to assess the relative importance of hydrocarbon accumulation in crabs from San Francisco and Eureka areas in relation to the decline in the Dungeness crab fishery in the San Francisco area. The initial phase in this investigation compared tissue hydrocarbon levels in Dungeness crabs from the San Francisco area with the same species of crab from the Eureka area in northern California where the crab fishery has not experienced a similar drastic decline. The second phase of this study identified the major hydrocarbons, including PAH, in San Francisco Bay juvenile crabs and sediments in areas where juvenile crabs occur. Sediment PAH were compared with tissue PAH of the juvenile crabs.

METHODS AND MATERIALS

Collection of Samples

For the first phase of the study, adult plus large and small juvenile Dungeness crabs were collected from San Francisco and Eureka areas (Figure 18). Both male and female crabs were included in the samples. The crabs were wrapped in aluminum foil and frozen until analysis. Adult crabs, approximately 130 to 170 mm carapace width (CW), excluding 10th anterolateral spines and estimated at 3 to 4 years old, were collected with crab traps from the ocean off San Francisco and Eureka. Juvenile crabs were collected from central San Francisco, San Pablo, and Humboldt Bays (Figures 60 and 16) by trawling and ringnetting during 1975 and 1976 and a sample of small crabs was collected by trawling in Humboldt Bay in 1979. Large juveniles ranged in size from approximately 70 to 100 mm CW and small juveniles ranged from approximately 30 to 60 mm. For comparisons with the field data, a sample of large juveniles was obtained from the Department of Fish and Game Marine Culture Laboratory (MCL) near Monterey in 1979. These crabs had been maintained in seawater at the laboratory after being collected as small juveniles in Humboldt Bay.

For the second phase, sediments were collected intertidally during a minus tide on May 23, 1978 along the east shore of San Francisco and San Pablo Bays in the vicinity of Red Rock Marina, Molate Point, and two sites at Pinole Point, east and west of the fishing pier (Figure 105). Duplicate sediment samples were collected at each site with a stainless steel spatula and 4-oz (118-g) jars with foil-lined lids, all of which had been washed in chloroform. Large juvenile crabs, approximately 70 to 110 mm CW, were collected during this phase by ringnetting at Pinole Point fishing pier and Red Rock Marina on April 26, 1978.

Sample Preparation

Adult and juvenile crabs were thawed and eggs, if present, were removed using solvent-washed instruments. The crabs were autoclaved at 10 psi for 10 min to denature enzymes. Adult and large juvenile crabs were dissected with solvent-washed instruments. Muscle tissue was removed from chelae and thorax, followed by removal of hepatopancreas tissue. Female gonadal tissue was taken when present. Small juveniles were ground whole with solvent-washed instruments for analysis. When several tissue samples were pooled from a given station, each set of tissues was placed in a solvent-washed jar and thoroughly

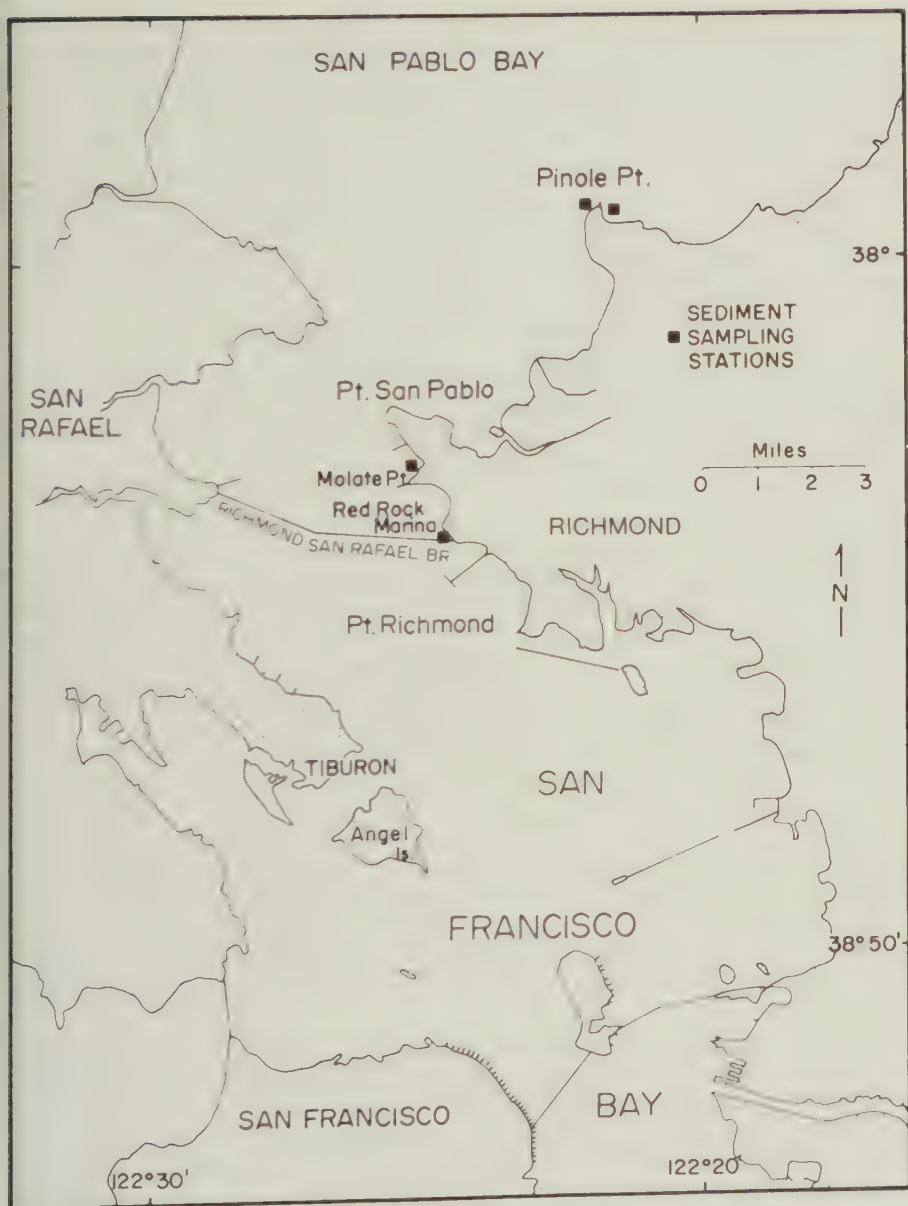


FIGURE 105. Sediment sampling stations in San Francisco and San Pablo Bays.

minced and mixed using solvent-washed scissors. In the first phase, tissues were dried to constant weight by spreading on clean aluminum foil in a drying oven for 48 hr at 60 C. Extraction of tissues was carried out by grinding in a solvent-washed mortar using grinding sand which had been ashed at 550 C to remove organic contamination. Each sample was ground with at least five changes of

glass-distilled hexane until the extracting solvent became colorless. Interfering polar compounds, primarily glycerides, were partially removed from extracts by passing them through a 2.5 x 25-cm glass column packed with silica gel from which organic contamination had been removed by ashing at 550 C. In the second phase an improved procedure was used. Crab tissues and sediments were lyophilized and extracted in chloroform by grinding with a sonic disintegrator (Tissuemizer, Tekmar Co., Cincinnati, Ohio). The chloroform extracts of tissue samples were saponified with 4N sodium hydroxide and the polar compounds were partially removed as in the first phase. The chloroform extracts of sediments were analyzed without saponification.

Analytical Procedures

Samples were concentrated by rotary evaporation and analyzed by thin layer chromatography (TLC) using methods from Guard et al. (1980). The saturates fraction containing the N-alkanes, isoalkanes, and cycloalkanes was quantitated by comparison with a gravimetrically prepared standard alkane mixture containing alkanes separated from three American Petroleum Institute (API) standard oils (Southern Louisiana crude, Venezuelan bunker, and Kuwait crude). The unsaturates fraction, containing aromatic and olefinic hydrocarbons, was quantitated by comparison with a composite aromatic hydrocarbon fraction separated from the three API oils. Standards were chromatographed on each TLC plate along with hydrocarbons extracted from crab tissues. Based on gravimetrically prepared standards, analyses of saturates, unsaturates, arenes, and total hydrocarbons showed average coefficients of variation of 13, 12, and 9%, respectively. Total hydrocarbons were determined with a relative error of 15%.

PAH levels were estimated by determining FAH levels using a Perkin-Elmer model 204A fluorescence spectrophotometer. Sample extracts were separated into saturates (alkanes) and unsaturates (including arenes) fractions using preparative TLC, and unsaturates were eluted from the silica gel into 4-ml chloroform prior to analysis. The fluorescent intensity of the chloroform solution of the unsaturate fraction was determined at 460 nm with excitation at 365 nm and compared to fluoranthene standards prepared by preparative TLC. FAH levels are reported as the equivalent amount of fluoranthene which produces an equal fluorescent intensity. The FAH represent the fraction of PAH which fluoresce at 460 nm when excited at 365 nm.

Gas chromatography (GC) was conducted on a Varian Aerograph Model 2740 gas chromatograph equipped with a flame ionization detector and a 1.5% OV-101 H/P Chromasorb G 100/120 mesh. The column temperature was held at 100 C for 2 min, then programmed to 275 C at 6 C/min. Gas chromatography/mass spectrometry (GC/MS) was conducted on a Finnigan 9500 gas chromatograph interfaced to a Finnigan 3100D quadrupole mass spectrometer via a single stage glass jet separator. Samples were injected onto a 5-ft x 2-mm (id) glass column of 3% OV-101 on 100/120 Gas-Chrom Q programmed from 100 C to 275 C at 6 C/min while the mass range of 12 to 460 amu was scanned in 3-sec cycles. Repeated procedural and solvent blanks were run to ensure the absence of detectable contamination.

The quantitative thin-layer technique determines non-volatile hydrocarbons, C₁₄ and above, with no interference from common chlorinated hydrocarbons. Small amounts of polar compounds including fatty acids, glycerides, phthalate

esters, and polar metabolites from hydrocarbons are separated in this analysis and are not included. While the data herein are internally comparable, caution must be applied when compared to data obtained by other techniques.

RESULTS

Phase I

Variation Between Sexes

A two way analysis of variance (Sokal and Rohlf 1969) was carried out using data from tissues of two male and two female large juvenile crabs from San Francisco Bay. The analysis showed no significant difference ($P > 0.05$) in hydrocarbon levels due to sex of the animals in either muscle or hepatopancreas tissue. Thus, data for males and females were pooled in subsequent calculations to provide increased statistical sensitivity.

Variation Between Areas

Adults and eggs. Averaged values of total hydrocarbon levels in muscle tissues of adult Dungeness crabs from San Francisco and Eureka areas did not exceed 50 ppm; but Eureka muscle tissue shows more than twice the total hydrocarbon content of the San Francisco crabs (Table 44). However, using the t-test at the $P \leq 0.05$ level, no significant differences could be demonstrated. FAH levels were quite low in both areas.

TABLE 44. Hydrocarbon Content of Adult Dungeness Crabs, *Cancer magister*, from San Francisco (SF) and Eureka (EU) Regions.

Tissue	Source	No. of determinations	Organisms pooled per determination	Hydrocarbon content ($\mu\text{g/g dry wt; mean} \pm \text{SD}$)			
				Saturates	Unsaturates	Total	FAH
Muscle.....	SF	2	6	$12 \pm 3^*$	$7 \pm 4^*$	19 ± 6	.002
	UE	4	4-5	31 ± 15	19 ± 19	50 ± 35	.004
Hepato-pancreas ..	SF	2	6	$82 \pm 2^*$	$56 \pm 13^*$	$138 \pm 15^*$	.010
	EU	4	4-5	22 ± 8	19 ± 11	41 ± 16	.010
Female gonad	SF	1	3	24	31	55	—
Eggs	SF	1	1	41	31	72	.001
	EU	2	3	$25 \pm 5^*$	$23 \pm 3^*$	$48 \pm 8^*$	.001

* = Range

For adult hepatopancreas tissue, total hydrocarbon levels averaged 138 ppm for San Francisco crabs, which was more than three times the averaged total for Eureka crabs. Both saturate and unsaturate fractions were significantly higher ($P < 0.01$) in San Francisco crabs. There were no differences in hepatopancreas FAH levels between the two areas, but these levels were an order of magnitude higher than muscle FAH levels, although they were still in the low ppb range (Table 44).

Eggs and gonadal tissue showed slightly higher average total hydrocarbon levels in San Francisco area crabs than in Eureka crabs. There were no differences between FAH levels in egg samples from the two areas. All of these levels, however, were in the same order of magnitude as those shown for muscle tissue (Table 44).

Large juveniles. Averaged results for hydrocarbons in juvenile crabs (Table 45) show that large juveniles from San Francisco Bay consistently had higher values for all categories of hydrocarbons than crabs from Humboldt Bay, with the exception of FAH in which there were no apparent differences by area. A Wilcoxon test (Sokal and Rohlf 1969) for two sample-ranked observations, not paired, was used to estimate statistical significance of the results. Saturated and total hydrocarbons in muscle tissue from San Francisco Bay were significantly greater than those from Humboldt Bay ($P \leq 0.05$), but differences in unsaturates were not significant. For hepatopancreas tissue none of the differences between San Francisco Bay and Humboldt Bay samples were significant ($P > 0.05$), probably because of the wide range in values in the San Francisco Bay samples.

All hydrocarbon levels including FAH in muscle tissue of laboratory-reared crabs were similar to those in large juveniles from Humboldt Bay. Hepatopancreas hydrocarbon levels were all considerably lower than in both San Francisco and Humboldt Bay large juveniles.

Small juveniles. Hydrocarbon levels in small juveniles cannot be compared directly with the other samples because small juveniles were analyzed whole. The levels in small juveniles in the two areas were similar except for the saturates which were appreciably higher in Humboldt Bay crabs (Table 45).

Variation Between Tissues

Values for total hydrocarbon content of muscle and hepatopancreas tissues were not significantly different (t-test, $P > 0.05$ level) for adult Eureka Crabs, and no significant difference was found between egg hydrocarbon values and combined muscle-hepatopancreas values. Using the same test, adult San Francisco crabs showed significantly higher levels of saturates, unsaturates, and total hydrocarbons in hepatopancreas tissue when compared with muscle, gonads, and eggs. No significant differences were found in these categories for FAH in either area.

In large juveniles, averaged total hydrocarbon levels in hepatopancreas tissues were significantly higher than muscle ($P \leq 0.05$) for both San Francisco Bay and Humboldt Bay crabs. Hepatopancreas FAH levels were also higher than muscle in both areas. There was, however, a wide range in individual values.

MCL crabs showed only a slight trend toward higher hydrocarbon levels in hepatopancreas tissue compared to muscle (Table 45).

Phase II

Sediment Hydrocarbons

Sediments from the eastern shore of San Francisco Bay contained appreciable amounts of saturates, unsaturates, and FAH (Table 46). The highest levels of hydrocarbons were found in sediments from Red Rock Marina; the lowest levels were in samples from east and west of Pinole Point. In each case the sediment-

TABLE 45. Hydrocarbon Content of Juvenile Dungeness Crabs, *Cancer Magister*, from San Francisco Bay (SFB), Humboldt Bay (HB), and Marine Culture Laboratory (MCL) Stock.

Tissue	Source	No. of determinations	Organisms pooled per determination	Hydrocarbon content ($\mu\text{g/g dry wt}$; mean $\pm$ SD)			
				Saturates	Unsaturates	Total	FAH
Large juveniles Muscle	SFB	5	4-5	48 $\pm$ 14	17 $\pm$ 13	66 $\pm$ 23	0.008 $\pm$.002
	HB	3	4-5	7 $\pm$ 1	11.7 $\pm$ 1.5	18.9 $\pm$ 0.2	0.005 $\pm$.0048
	MCL	1	4	6.5	13.2	14.7	0.002
Hepatopancreas	SFB	5	4-5	397 $\pm$ 257	114 $\pm$ 100	511 $\pm$ 315	0.016 $\pm$.016
	HB	3	4-5	218 $\pm$ 10	87 $\pm$ 25	305 $\pm$ 35	0.021 $\pm$.017
	MCL	1	4	22.8	20.3	43.1	0.005
Small juveniles Whole	SFB	1	ca. 10	47	31	77	0.006
	HB	1	ca. 10	118	38	155	0.007

associated oil was rich in unsaturates (predominantly aromatic) hydrocarbons. The unsaturates comprised 33 to 51% of the total hydrocarbons. FAH accounted for only 2 to 8% of the unsaturates indicating that they contained high amounts of alkylated monocyclic and bicyclic aromatics suggestive of petroleum origin.

TABLE 46. Hydrocarbons in Extracts of Sediment from San Francisco and San Pablo Bays.

Location	No. of samples	Mean hydrocarbon content ($\mu\text{g/g}$ dry wt; mean $\pm$ range)			
		Saturates	Unsaturates	Total	FAH
Red Rock Marina	2	534 $\pm$ 4	551 $\pm$ 12	1085 $\pm$ 16	45 $\pm$ 5
Point Molate	2	119 $\pm$ 11	72 $\pm$ 10	191 $\pm$ 1	4 $\pm$ 1
Pinole Point					
West	2	22 $\pm$ 17	15 $\pm$ 1	37 $\pm$ 16	0.4
East	2	37 $\pm$ 6	27 $\pm$ 14	16 $\pm$ 20	0.54 $\pm$ 0.02

GC analysis of the Pinole Point extracts (Figure 106) shows a complex range of compounds from C_{16} to C_{32} . Several n-alkanes (denoted by carbon numbers) were identified as well as the polynuclear aromatics fluoranthene and pyrene. The saturates fraction purified by preparative TLC shows a predominance of branched and cyclic compounds (unresolved complex mixtures) with n-alkanes in evidence as noted (Figure 107). This mixture is characteristic of oil of petroleum origin plus some biogenic n-alkanes in the C_{25} to C_{31} range. The unsaturates fraction, also purified by preparative TLC, contained a wide range of compounds (Figure 108); therefore, a narrow cut of aromatics containing 3- and 4-ring compounds was purified. The gas chromatogram of this fraction (Figure 109) shows numerous PAH.

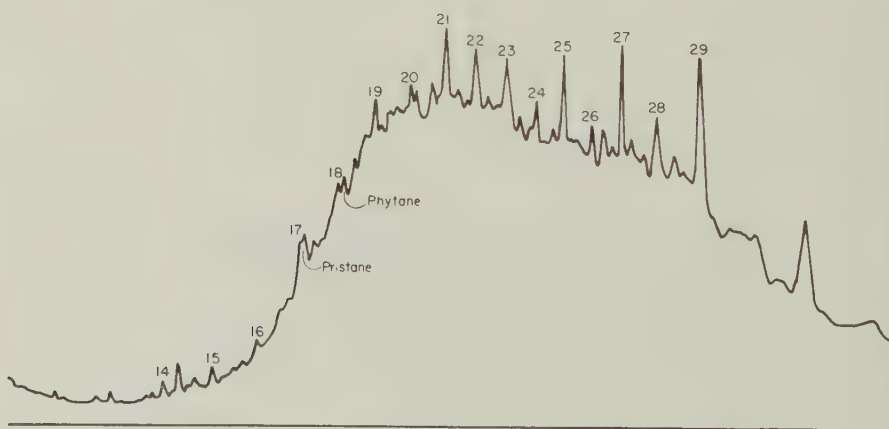


FIGURE 106. Gas chromatogram of sediment associated hydrocarbons from Pinole Point, San Francisco Bay.

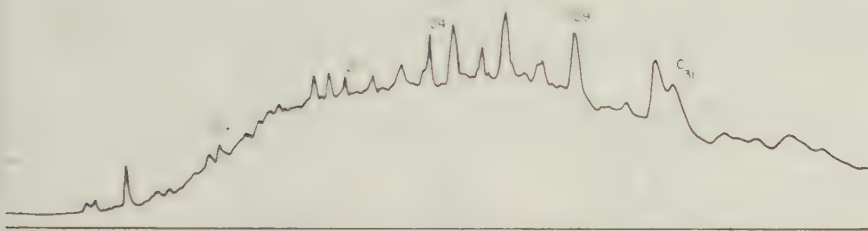


FIGURE 107. Gas chromatogram of saturates fraction from Pinole Point sediment. Numbers refer to carbon numbers of n-alkanes.

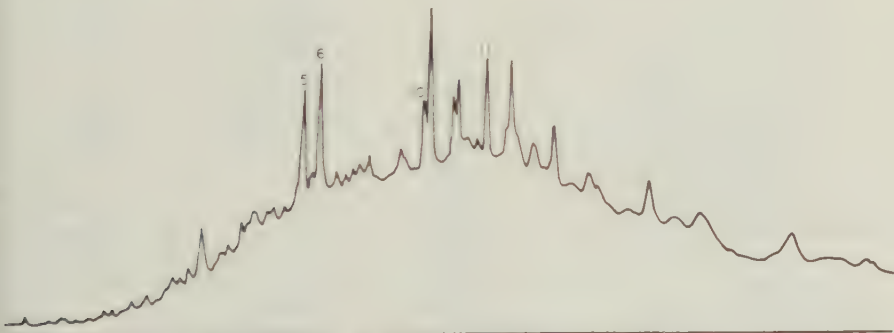


FIGURE 108. Gas chromatogram of unsaturates fraction from Pinole Point sediment. Numbers refer to compounds in Table 47.

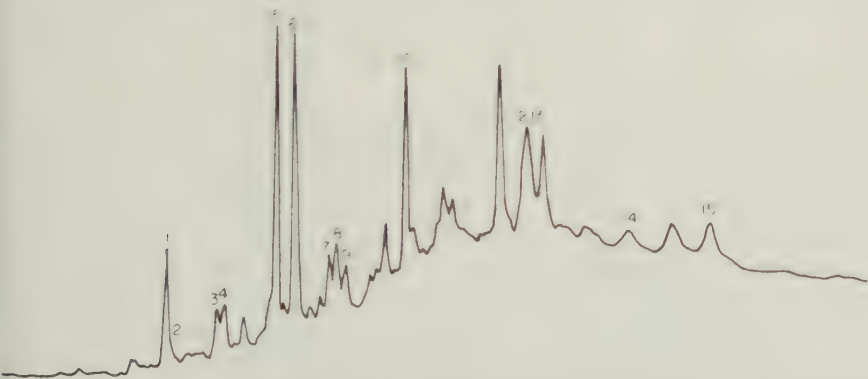


FIGURE 109. Gas chromatogram of 3- and 4-ring aromatic hydrocarbons fraction from Pinole Point sediment. Numbers refer to compounds in Table 47.

Altogether, 17 PAH were identified (Table 47). These include the mammalian carcinogens benzo(a)pyrene, benzo(b)pyrene, benzo(g,h,i)perylene, and, in addition, microbial mutagens chrysene and 1-,2-benzanthracene.

TABLE 47. Carcinogenicity/Mutagenicity of Polynuclear Aromatics Identified in Sediment-associated Oil from Molate Point, California.

Peak no. (Fig. 109)	Compound	Identification *	Carcinogenicity †	Mutagenicity ‡
1	Phenanthrene	C	0	0
2	Anthracene	T	0	0
3,4	Methylphenanthrenes (2)	C	Unknown	Unknown
5	Fluoranthene.....	C,P	0	Unknown
6	Pyrene	C	0	0
7,8	Benzofluorenes (2)	C		Unknown
9	Phenyl dimethylnaphthalene	C		Unknown
	{ Chrysene ‡		+	+
10	{ 1-,2-Benzanthracene ‡	C	+	+
	{ Triphenylene ‡		0	Unknown
11	Benzofluoranthenes	C	Unknown	Unknown
12	Benzo(a)pyrene.....	C	++	+
13	Benzo(b)pyrene	C	+++	+
14	Diphenylnaphthalene	C	Unknown	Unknown
15	Benzo(g,h,i)perylene	C	++	Unknown

* C = Confirmed by gas chromatography/mass spectroscopy (GC/MS). T = tentative by GC only, P = proven by fluorescence spectroscopy.

† Dipple (1976); McCann and Ames (1976); McCann et al. (1975): 0 = not carcinogenic/mutagenic; + = carcinogenic/mutagenic; +++ = highly carcinogenic/mutagenic.

‡ Not separated by GC.

To ascertain the probable source of these compounds, we examined PAH profiles from several sources (Figure 110). The profile of five predominant PAH from Pinole Point sediment most closely resembles that reported for street dust (Giger and Schaffner 1978) and is not similar to crude oil or distillate fuel.

Crab Tissue Hydrocarbons

The levels of hydrocarbons found in muscle tissue of crabs from Pinole Point and Red Rock Marina (Table 48) were not appreciably above our detection limits for saturates, unsaturates, or FAH. These levels were slightly lower than those found in the first phase. Levels of saturates and unsaturates of hepatopancreas tissue were significantly higher than muscle tissue ($P \leq 0.05$), following the trend noted in the first phase. From the appearance of the TLC plates, it is probable that the unsaturates of the hepatopancreas contained appreciable quantities of olefinic material of biogenic origin. Generally, the levels of FAH in hepatopancreas tissue were higher than those found in muscle. These hepatopancreas FAH levels, although an order of magnitude higher than those found in Phase I large juveniles, were still in the ppb range.

The gas chromatogram of the PAH fraction of hepatopancreas unsaturates (Figure 111) is noticeably dissimilar to that fraction from the sediments (Figure 109). GC/MS analysis indicates that the major components of the PAH fraction isolated from the hepatopancreas are unsaturated hydrocarbons and contaminants (trimethylsilyl ethers and oxygenated hydrocarbons). No evidence of sediment PAH was found in the crab tissues.

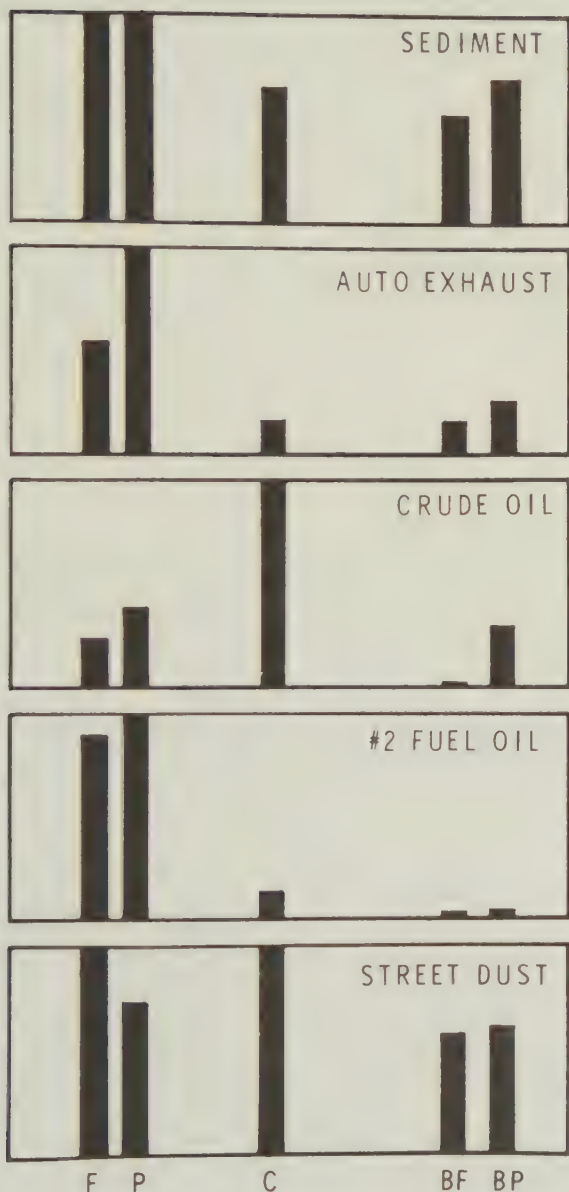


FIGURE 110. PAH profiles from various sources (Modified from Giger and Schaffner (1978). F = fluoranthene; P = pyrene; C = sum of chrysene, 1-, 2-benzanthracene and tri-phenylene; BF = benzofluoranthenes; BP = sum of benzopyrenes.

TABLE 48. Mean Hydrocarbon Content of Juvenile Dungeness Crabs Collected Near Sediment Stations in San Francisco and San Pablo Bays.

Location	Mean hydrocarbon content ($\mu\text{g/g}$ dry wt; mean $\pm$ SD)				FAH
	Tissue	Saturates	Unsaturates	Total	
Pinole Point	Hepatopancreas (M & F) *	192 $\pm$ 132	78 $\pm$ 77	270	0.15 $\pm$ 0.18
Red Rock Marina	Hepatopancreas (M)	244 $\pm$ 135	88 $\pm$ 47	332	0.27 $\pm$ 0.25
Pinole Point	Muscle (M & F)	5 $\pm$ 9	6 $\pm$ 9	11	0.07 $\pm$ 0.12
Red Rock Marina	Muscle (M)	5 $\pm$ 7	5 $\pm$ 6	10	0.004 $\pm$ 0.009

* M = male, F = female



FIGURE 111. Gas Chromatogram of 3- and 4-ring aromatic hydrocarbons fraction from a Dungeness crab hepatopancreas.

DISCUSSION

In this study we determined the levels of saturated and unsaturated hydrocarbons in tissues of Dungeness crabs from various locations. These compounds are prevalent in petroleum and related products, but also are produced by some marine organisms. Therefore, the presence of hydrocarbons in crab tissues does not prove contamination by petroleum residues, nor does absence of PAH (included in the unsaturates) demonstrate the pristine character of tissue because there is evidence that these hydrocarbons can be metabolized by certain crustaceans (Lee et al. 1976). However, we believe that abnormally high levels of petroleum-like hydrocarbons constitute evidence of petroleum contamination. Exceptions might arise when very high levels of naturally-occurring hydrocarbons are present, perhaps during heavy phytoplankton blooms.

Hydrocarbon levels determined by TLC in several other species of crab (Table 49) support this contention. For example total hydrocarbon levels in the muscle or hepatopancreas tissue of the rock crab, *Cancer antennarius*, did not exceed 78 ppm among two coastal "cleanwater" areas south of San Francisco. Based on comparison between samples from "clean" and "more highly contaminated" areas, we feel that hydrocarbon concentrations well above 50 ppm for the saturates fraction and 25 ppm for the unsaturates fraction generally

TABLE 49. Hydrocarbon Content of Crabs from the Central California Coast, an Offshore Island, and Bays.

Location	Species *	Tissue †	Hydrocarbons ($\mu\text{g/g}$ dry wt)		
			Alkane	Aromatic	Total
Coast					
Santa Cruz Pier	CA	h	<7	<7	<14
		m	nd‡	nd‡	
Pigeon Pt.	CA	h	52	26	78
		m	18	<7	<25
E. Farallon Island	CM	h	80	43	123
		m	14	11	25
Tomales Bay	HO	t	<1.4	nd‡	
	HO	t	14	2	16
San Francisco Bay					
Oakland Harbor	CA	h	231	81	312
		m	30	8	38
North Bay	CA	h	75	43	118
		m	30	11	41
North Bay	CA	h	193	57	250
North Bay Shore	HO	t	20	7	27
Pt. San Pablo	PS	e	1540	1460	3000

CA = *Cancer antennarius*; CM = *Cancer magister*; HO = *Hemigrapsus oregonensis*; PS = *Pagurus samuelis*.

h = hepatopancreas; m = muscle; e = egg mass; t = entire (total) organism.

nd = no data

suggest petroleum hydrocarbon pollution. On the basis of this criterion we find no evidence for appreciable petroleum contamination of adult crab muscle tissue from either the San Francisco or Eureka fishery areas.

We have found in this study that tissues of crabs from areas believed to receive lower inputs of petroleum hydrocarbons (e.g. northern California coastal crab population; MCL crab stock) had total hydrocarbon levels below 50 ppm in all tissues examined.

Crabs obtained from areas believed to be subjected to higher inputs of petroleum had the highest levels of saturates and unsaturates in hepatopancreas tissue. These levels suggest contamination by petroleum residues. Both adult and large juvenile Dungeness crabs in the San Francisco area carry larger burdens of hydrocarbons in their hepatopancreas tissue than comparable crabs from the Eureka area. Also, large juveniles in both San Francisco and Humboldt Bays carried larger burdens than their adult offshore counterparts. The petroleum-like compounds generally were found concentrated in the hepatopancreas tissue with little or no contamination of muscle tissue. No clear trends were seen for PAH which were generally in the low ppb range. San Francisco Bay large juveniles from Phase I (Table 45) showed slightly elevated total hydrocarbon levels in muscle tissue compared to Humboldt Bay, but later samples (Phase II) from San Francisco Bay (Table 48) were lower than Phase I Humboldt Bay samples. These observations indicate that contamination of crab muscle tissue by petroleum hydrocarbons is minor in the worst case.

The high levels of unsaturated compounds (56 ppm) in the hepatopancreas tissues of adult crabs from the San Francisco area was of interest based on their offshore habitat, away from polluted Bay sediments. These may have resulted

from the presence of olefinic material (not petroleum) from natural sources, or these crabs may have resided in San Francisco Bay as juveniles (Tasto, Chapter 10; Collier, Chapter 11). The high values for Humboldt Bay juvenile crabs, compared to MCL stock, may reflect some contamination of Humboldt Bay by petroleum residues from oil spills or land run-off. A portion of the high levels of total hydrocarbons ($\bar{x} = 511$ ppm) found in the hepatopancreas tissues of San Francisco Bay juveniles is almost certainly of pollutant origin. Although direct comparisons are difficult, low general values for small juveniles and higher values for large juveniles suggest that hydrocarbon burdens were acquired as a time or site dependent environmental process.

The GC/MS analysis of the "3- to 4-ring polynuclear aromatic fraction" of the unsaturates in large juvenile hepatopancreases in Phase II did not show accumulation of sediment PAH but only the presence of olefinic materials of potential biogenic origin (and analytical artifacts). Therefore, while the hepatopancreas appears to retain petroleum-like saturated hydrocarbons at levels indicating petroleum contamination, the toxic PAH are not accumulated to any appreciable extent.

Because there are no known overt kills of crabs in San Francisco Bay and our specimens were taken alive and in apparently healthy condition, it is presumed that any effects of elevated levels of petroleum hydrocarbons on the Dungeness crab would be chronic and sublethal. A study by Krebs and Burns (1977) includes a summary review of the small amount of existing information on sublethal effects of hydrocarbons on crabs. Their studies of long term effects of an oil spill on salt-marsh fiddler crabs, *Uca pugnax*, which contained levels of up to 280 ppm tissue hydrocarbons (whole body levels of petroleum-derived hydrocarbons only), showed reduced crab density, reduced ratios of males to females, reduced juvenile settlement, heavy overwinter mortality, and behavioral anomalies. These levels are considerably higher than the whole body levels including both biogenic and petroleum-derived hydrocarbons (Table 45) we found in small juvenile Dungeness crabs.

We identified specific PAH present in San Francisco Bay sediments and analyzed San Francisco Bay juveniles for the presence of these PAH in their tissues. PAH represent the most toxic class of petroleum hydrocarbons and have been shown to exert sublethal effects in the low ppb level in receiving water.

Sediment-associated oil from the San Francisco Bay samples is rich in unsaturated (predominantly aromatic) hydrocarbons. This result, together with the low values, 2 to 8% of the unsaturates for fluorescent aromatics, is consistent with the presence of highly alkylated monocyclic and bicyclic aromatics, such as would be found in weathered lubricating oils. This suggests that a major input to San Francisco Bay may be waste lubricating and crankcase oil. The aromatic (unsaturate) fraction, analyzed by GC (Figure 108), shows a large unresolved complex mixture which is also typical of lubricating oil. However, the 3- and 4-ring PAH compounds show a pattern of major components typical of combustion source. This supports the suggestion of Giger and Schaffner (1978) that street dust which includes auto exhaust components may be an important source of petroleum hydrocarbons in aquatic environments.

Our analysis of Pinole Point sediments suggests that water runoff from the land is a major input of petroleum hydrocarbons to the Bay. Hydrocarbons in runoff are from lubricating oils and atmospheric fallout, to which auto exhaust is a

major contributor. If this suggestion is correct, then the PAH we identified enter the marine environment in the particulate phase. Previous laboratory studies (DiSalvo et al. 1977) have indicated little or no uptake of sediment-associated oil by organisms. The lack of accumulation of sediment PAH into Dungeness crab hepatopancreas and muscle tissue is consistent with this result, although it is possible that the reported ability of crustaceans to metabolize aromatic hydrocarbons (Lee et al. 1976) can also account for the lack of accumulation. However, Burns (1976) concluded that the fiddler crab, *U. pugnax*, had only a minimal ability to metabolize "foreign" hydrocarbons. As a result, the oil hydrocarbons in body tissue were similar to those in marsh surface mud in an area heavily polluted from an oil spill.

We show evidence for accumulation of hydrocarbons in the hepatopancreas of Dungeness crabs, but not sediment-associated PAH. If uptake of sediment-associated aromatic hydrocarbons does occur in the Dungeness crab then it follows that these hydrocarbons are metabolized. This raises the question of whether a requirement for metabolizing hydrocarbons and products of this metabolism would affect population dynamics of the Dungeness crab.

We did not study water soluble hydrocarbons, although there is some evidence from laboratory studies that these can cause sub-lethal effects on crustaceans at low ppb levels in water (Katz 1973; Kittredge et al. 1975). Further studies on the significance of water soluble hydrocarbons to the Dungeness crab may be warranted.

Results of our study support several important conclusions regarding effects of petroleum pollution on the Dungeness crab. First, the muscle tissue appears free from appreciable petroleum contamination even in crabs from areas receiving considerable petroleum input. Second, elevated levels of petroleum-like hydrocarbons found in the hepatopancreas tissue of crabs from both San Francisco and Humboldt Bays suggest that these crabs have accumulated petroleum hydrocarbons. Third, while the sources for elevated PAH concentrations in crab hepatopancreas were not identified, the PAH accumulated in hepatopancreases were not similar to those in sediments. Whether this is due to lack of uptake or metabolism by the crabs is not known. Fourth, whether there is any long-term impact due to sublethal effects on the crab population from sediment-associated or other saturated hydrocarbons, or metabolites of aromatic hydrocarbons, remains unknown.

Chapter 21

LABORATORY CULTIVATION OF THE DUNGENESS CRAB, *CANCER MAGISTER*

by

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INTRODUCTION

Research on mass cultivation of the Dungeness crab, *Cancer magister*, was initiated at the Marine Culture Laboratory (MCL) in 1971 (Ebert et al. 1974). This research continued seasonally at low levels through 1974, and findings in part, although not appearing in the primary literature, were presented through various California Department of Fish and Game reports (e.g., Ebert et al. 1975). In 1974, when the State Legislature directed the Department to investigate the decline of the Dungeness crab fishery off central California (Farley, Chapter 2), these mass-cultivation efforts were intensified.

This paper describes the culture studies conducted with each of the life stages of the Dungeness crab. These studies underwent progressive refinement over a span of 9 years (1971–1980). The studies are presented in terms of this evolution because some of the early techniques affected the results of later studies.

An integral part of these intensified culture efforts was research to develop a small-scale mass culture system that could yield determinate numbers of larval (and subsequently juvenile) crabs for bioassay and mariculture studies. In 1976 a prototype, small-scale, larval culture system was assembled and tested. Efforts prior to 1976 are described very generally; studies after development of the small-scale system are described in greater detail.

LITERATURE REVIEW

Snow and Neilsen (1966) described premating and mating behavior of the Dungeness crab. MacKay (1934) and Buchanan and Milleman (1969) described the Dungeness crab prezoea, a very brief stage which emerges from the egg upon hatching and exists for 10 to 15 min prior to the stage I zoea. Poole (1966) was first to cultivate all larval stages although he did not observe the prezoeal stage. Reed (1969) investigated optimal temperature and salinity requirements for zoeal stages and provided information on zoeal stage cultivation methods in flasks. Gaumer (1971) investigated larval and juvenile culture requirements and effects of various physical factors on growth, lighting, substrates, aeration, swimming behavior, and diets. Brugman (1972) investigated the effects of temperature on the growth of juvenile Dungeness crabs.

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Rice and Williamson (1970) reviewed general methods for rearing larval decapod crustaceans. Buchanan et al. (1975) described a flowing-water apparatus for the culture of brachyuran crab larvae and Hartman (1977) designed and evaluated a mass rearing system for culturing brachyuran crab larvae. Hartman's culture apparatus employed an upwelling design that could operate on either a flow-through or recirculating mode.

Dungeness crab diseases, in general, are treated by Fisher (1977a). Armstrong and Fisher (1977) reviewed the fungal infection *Lagenidium* sp. in the Dungeness crab. Fisher (1977b) discussed *C. magister* microbial epibionts and Wickham and Fisher (1977) and Wickham (1979a and 1979c) investigated nemertean worm infestations in Dungeness crab egg masses.

ADULT STUDIES

Methods and Materials

Collecting and Transporting

Adult brood stock was obtained from crab fishery areas off California, Washington, and Alaska, although most came from San Francisco or Eureka-Crescent City areas (Figure 18). We obtained later egg-bearing (ovigerous) crabs from Washington and Alaska when egg-bearing crabs were no longer seasonally available off California.

Crabs typically were caught in crab pots by commercial fishermen and on one occasion by trawl. In California, we also had the assistance of Department vessels and biologists from other units who set crab pots specifically to capture brood stock.

The crabs generally were wrapped in seawater-saturated cheesecloth, towel-ing, or burlap, and packed in styrofoam containers for shipment to the laboratory. Refrigerant bags were placed in each container to maintain cool temperatures and alleviate possible heat stress to the crabs. On one occasion ovigerous crabs were transported from the San Francisco region by automobile in chilled, aerated seawater. A companion group was packed in the usual method described above. On another occasion ovigerous crabs were left refrigerated overnight; the out-of-water period exceeded 24 hr. Crabs from Alaska, Washington, and northern California were transported by air and those from the San Francisco region by automobile.

Holding

Crabs were examined and measured (carapace width) upon arrival at the laboratory. Particular attention was focused on each egg mass, its size, and coloration. Female crabs usually were isolated in individual 73-liter aquaria with or without (usually without) a sandbed. Ambient-temperature seawater, sand-filtered to about 20 μ m and ultraviolet-treated (UV-treated), was supplied to each aquarium. Water flow rates were not closely monitored, but typically exceeded 7 to 8 liters/min. A few adult male crabs were shipped to the laboratory and less attention was given to their disposition. They often were maintained in a common holding tank with or without a sandbed.

Generally, after the larvae hatched, we deposited the female in a common holding tank and individual identity data were not maintained. However, recognizing that certain parent crabs produced more viable offspring, we eventually

isolated and maintained the identity of some of these for future breeding studies.

After 1976, we compartmentized a number of holding tanks. Compartments for individual crabs were approximately 30 by 57 cm. Compartments for mating pairs were larger (42 by 55 cm). Compartmented tanks generally had sand substrates with subsand filtration.

A coding system was devised to identify individual crabs. This system allowed us to trace individual crab life histories in the laboratory (i.e., moltings, growth increments, and matings).

Feeding

Adult crabs generally were maintained on a frozen market squid, *Loligo opalescens*, diet supplied fresh on alternate days. When larvae commenced to hatch, the market squid diet was suspended.

Egg Mass Observations

Daily observations were made of egg shedding and egg mass coloration; coloration is indicative of embryo development within the egg. Three color descriptions were used: yellow-orange, orange, and brown (representing, respectively, the least advanced to most advanced embryo developmental stages). As developing embryos approached maturity, either the water flow was discontinued at night and aeration provided to avoid larval loss, or a screened, polyvinylchloride (PVC) pipe section partially immersed in seawater was positioned beneath the hatching tank overflow to collect larvae.

Mating

Selection of mature adult crabs for mating was based on crab size and female molting-cycle stage. Cleaver (1949) found that the smallest mature female crab was 72-mm carapace width (CW). Wild (Chapter 15) found that all females over 110 mm CW were mature. Butler (1960) reported that all male crabs 116 mm CW and larger were sexually mature. For laboratory matings, we only used crabs exceeding 100 mm CW. Females were selected for mating just prior to molting, or immediately following while still in a soft-shell condition.

A male-female pair to be mated was put in a common compartment. Premating, mating, and post-mating behavior were observed and noted. After mating, male crabs were returned to their compartment; female crabs remained in the mating compartment. Strict sanitary practices were implemented to keep these mating compartments clean (e.g., daily removal of excess food and siphoning of bottom debris).

Spawning, Egg Development, and Hatching

After mating, female crabs were examined periodically for egg deposition (spawning). After spawning, egg development was closely monitored. When developing crab embryos were near-term, females were transferred to the same kind of hatching tanks used for wild population ovigerous crabs.

Water temperature during the egg incubation period was recorded daily for seven crabs. Water temperatures for each of these crabs was summed and reported as "total integrated temperature". This method was used to examine the relationship between temperature and crab embryo development rate. Theoretically, small variations (range) in total integrated temperatures indicate a positive relationship between temperature and embryo development rate;

wide variations suggest little relationship between these factors. Letritz (1959) considered this concept for estimating the incubation period in trout eggs, and Kikuchi and Uki (1974) used it for measuring gametogenesis in Japanese abalones.

After larvae hatched, adult female crabs were returned to their original compartments. Observations were made to determine if a female crab would spawn a second or third time without mating or molting.

Results

Collecting and Transporting

Crabs transported out of water, but kept moist and cool, typically arrived at the laboratory in a lethargic state; they become active following immersion in seawater. Crabs transported in chilled seawater arrived in an active state and seemingly had undergone less stress.

Crab transit periods ranged from 5 or 6 hr in the San Francisco region to nearly 20 hr from Alaska. The refrigerated, egg-bearing crabs maintained overnight usually survived the ordeal; however, their near-term embryos apparently were severely stressed and very few live larvae hatched. These larvae were discarded.

Holding

Ovigerous crabs were relatively easy to maintain in the laboratory although some died. Cause of death possibly was due to shock stress while in transit, injuries sustained in handling, or a combination of both.

Feeding

Adult crabs displayed variable behavior in their feeding habits during the egg-bearing period. They fed voraciously at times, and on other occasions exhibited total indifference to introduced market squid.

Egg Mass Observations

Ovigerous crabs shipped to the laboratory typically had orange- to brownish-colored egg masses. On occasion, larvae commenced to hatch on the day following the adult crabs' arrival. More often, crabs did not commence to hatch larvae until they had been in the laboratory for 2 to 6 weeks. During this period they frequently tended their egg masses with their posterior-most dactyls. As a result, substantial portions of egg masses were, at times, torn away.

The nemertean worm *Carcinonemertes errans* commonly was present in most egg masses. Some egg masses had heavy infestations; however, we made no attempt to compare the extent of worm infestation to crab origin. We compared crab larval hatching success from the Eureka-Crescent City region with those from San Francisco and found no significant difference in hatching success (Ebert et al. 1975).

Egg masses of laboratory-maintained crabs, fed only squid during ovary development, were typically a greyish-white color. This was found to be a dietary response to a lack of carotin pigment, of which squid have only a trace (Goodwin 1960). A squid diet supplemented with shrimp, sea urchin, or mussel produced normal orange-colored egg masses. The greyish-white egg masses apparently developed normally and gradually took on a brownish hue due to crab embryo pigmentation.

Egg masses of laboratory-maintained crabs frequently were contaminated by bacteria, a fungus, ciliate protozoans, and a nemertean worm. Bacterial and ciliate contamination was particularly evident in crabs that produced second or third egg masses without mating or molting after their initial spawn.

Mating

Pre-mating, mating and post-mating behavior generally followed the behavior pattern described by Snow and Neilsen (1966). Our controlled crab matings commenced in 1975. These controlled matings were accomplished during 9 different months, with a maximum of four in September. Of 24 controlled mating attempts, four females were cannibalized after they had molted, and six crab pairs apparently did not mate successfully because the females failed to spawn. The remaining 14 matings were successful; however, only six of these ultimately resulted in larval hatches. The remaining eight crabs either had poor spawns that formed small, apparently contaminated egg masses that gradually disintegrated (five cases), or the female spawned in a compartment that lacked a sand substrate. Sand substrate is necessary for the crab to form an egg mass.

Spawning, Egg Development, and Hatching

Crab spawnings from controlled matings spanned 4 months with October being the peak month in which six spawnings occurred. In five cases, crabs spawned without having mated or molted from the time of their last spawning. Two of these crabs spawned a second time without mating or molting. Another crab spawned after molting, but without mating since her last spawning. However, only one of the crabs that had not mated or molted since a prior spawning produced a viable egg mass that ultimately resulted in a successful hatch.

The time from mating to spawning for 14 crabs averaged 163 days (range 81 to 391 days). The time from spawning to larval hatch for seven laboratory-maintained crabs averaged 75 days (range 61 to 101 days). Total integrated temperature (sum of temperatures) from the time of spawning to hatch initiation for these seven crabs averaged 914 C (range 656 to 1105 C) (Table 50).

Individual crab hatching durations were similar for all crabs originating from California. They were not measured for crabs originating elsewhere. The duration of a larval hatch per adult averaged about 8 days (range 5 to 12 days). The number of larvae hatched daily per adult, although variable, followed a characteristic pattern. Typically, the hatch was small on the 1st day (4% of total), increased markedly on the 2nd day, peaked on the 3rd or 4th day, then tapered off to approximately the 1st day's level by the 6th day.

Hatching success determined for 15 field-caught ovigerous crabs averaged about 607,000 larvae per crab (range 230,500 to 1,122,400 larvae) (Ebert et al. 1975). Hatching success for laboratory-mated crabs averaged 103,000 larvae (range 38,600 to 184,000 larvae) (Table 50).

Discussion

Crab shipping methods generally were adequate. Occasionally, crabs were not insulated sufficiently from the chiller bags and died. A few crabs died from heat stress. Crab embryos on egg-bearing adults appeared to be less tolerant of transit stresses than the adult, particularly late-term embryos. Shipping these crabs in chilled (10–12 C) seawater may alleviate stress but is not practical. We

TABLE 50. Reproductive Data For Laboratory-maintained Dungeness Crabs, 1975-1978.

<i>Female Carapace width (mm)</i>	<i>Date mated</i>	<i>Date spawned</i>	<i>Time to hatch (days)</i>	<i>Total* integrated temp (C)</i>	<i>Estimated larval hatch</i>	<i>Remarks</i>
128.0	09/06/75	10/01/76	-	-	-	Small whitish-colored egg mass; failed to develop.
119.5	09/08/75	12/23/75	101	1105	91,900	Male cannibalized female. Male had mated earlier (10/05/75).
129.5	11/20/75	-	-	-	-	Eggs deposited on tank floor; failed to develop; no sand substrate.
124.6	12/10/75	10/01/76	-	-	-	Male cannibalized female.
-	12/22/75	-	-	-	-	Eggs deposited on tank floor; failed to develop; no sand substrate.
130.7	01/06/76	10/13/76	-	-	-	Eggs deposited on tank floor; failed to develop; no sand substrate.
139.4	01/19/76	11/03/76	-	-	-	Male cannibalized female.
123.6	03/26/76	-	-	-	-	Whitish-colored egg mass; failed to develop; contaminated.
136.2	05/17/76	10/05/76	-	-	-	Normal egg mass. Good larval hatch.
132.5	06/29/76	10/25/76	66	993	-	Small egg mass; failed to develop; disintegrated by 12/76.
-	08/13/76	11/09/76	-	-	-	Small, pinkish-colored egg mass; failed to develop.
113.9	08/20/76	11/09/76	-	-	-	Small, whitish-colored egg mass; failed to develop.
-	09/29/76	01/07/77	-	-	-	Male cannibalized female.
104.8	11/09/76	-	-	-	-	Large, whitish-colored egg mass.
-	05/11/77	11/14/77	61	771	-	Crab had not mated or molted since prior spawning.
132.5	not mated	04/29/77	62	656	-	Eggs deposited on tank floor; failed to develop; no sand substrate. Crab
139.4	not mated	03/20/77	-	-	-	had not mated or molted since prior spawning.
139.4	not mated	11/01/77	-	-	-	Whitish-colored egg mass deposited on sand; failed to develop. Repre-
152.8	not mated	11/02/76	-	-	-	sented second spawning without having mated or molted.
152.8	not mated	03/28/77	-	-	-	Eggs deposited on tank floor; failed to develop; no sand substrate. Crab
141.7	not mated	11/14/77	-	-	-	had not mated or molted since prior spawning.
114.0	06/20/78	10/06/78	75	912	184,000	Same crab cited above. Eggs deposited on tank floor; failed to develop;
105.0	07/26/78	11/11/78	84	1028	38,600	no sand substrate. Total of 146 days between spawnings. Crab had not
105.1	09/02/78	12/24/78	78	932	97,600	mated or molted.
						Molted on 03/01/77, but was not mated. Egg mass small; last observed
						on 01/12/78; fate unknown.
						Larvae died as prezoaeae.
						Larvae died as prezoaeae.
						Larvae died as prezoaeae.

* Sum of daily temperatures for the egg incubation period.

had considered shipping crabs in sealed plastic bags containing seawater-saturated sponges in an oxygen-saturated atmosphere, all packed in a styrofoam container with chiller bags. This is a standard method for other shellfish species. However, crab dactyls and chelae pose a problem with this method unless extra-thick or double-layered bags are used.

The role of the nemertean worm *C. errans* in crab egg masses is not fully understood. Wickham (1979a) sampled Dungeness crab egg masses during four spawning seasons. He estimated that annual crab-egg mortality from worm predation averaged about 55% and 28% in central and northern California, respectively, and could have contributed to the prolonged collapse of the central California fishery. However, information is lacking on the relationship between the number of crab eggs spawned in nature and hatching success. As pointed out earlier, we found that crab hatching success in the laboratory was not significantly different for females from central and northern California. Likewise, it is not known whether *C. errans* preys on healthy or aberrant eggs, or both.

A related nemertean worm *C. carcinophila* reportedly eats eggs of the blue crab, *Callinectes sapidus*, but even heavy infestations are thought to have little effect on crab production (Overstreet 1978). The blue crab produces over 2 million eggs and may do this twice annually (Overstreet 1978). The Dungeness crab produces from 1 to 2 million eggs per spawning (Mayer 1973) and this is thought to be an annual event (Waldron 1958). Although we observed that two annual spawnings were not uncommon in laboratory-maintained Dungeness crabs, the second egg mass was small and may have been anomalous.

The mating period for Dungeness crabs off California generally peaks during the May-June period. We did controlled matings over a 9-month period with a maximum of four in September. The results of controlled crab matings were highly variable, but revealed some interesting data. In those four cases where the male crab cannibalized the female, it appeared that the male crab was unable to service the female. One of the females was cannibalized by a male which had successfully mated with another female 3 months earlier. It is not known how long spermatogenesis takes. If it is longer than 3 months, which it may be in a laboratory setting, then this could account for the unsuccessful matings.

Of the six successful hatches from our controlled matings, four occurred in May, June, or July, the remaining two in September. Under natural conditions in central California, crab hatching usually occurs during late December to March. One of our September matings that resulted in a successful hatch was with a female crab that was captured as a megalopa in June 1974, reared at the laboratory, and reached sexual maturity in September 1975 (Instar XI). Under natural ocean conditions this crab probably would have developed faster, reached sexual maturity 2 or 3 months earlier, and spawned the first time about October, approximating the natural population reproductive period. Our results suggest that the crab hatching period in the laboratory can be extended a few months beyond that of the natural population. This could be a valuable asset to crab cultivation studies.

The long period between mating and spawning for two crabs (307 and 391 days) suggests that these crabs may have had immature ova and delayed spawning until the following spawning season peak (October). This served to distort the expected time of 4 to 5 months between crab mating and spawning.

The time from spawning to hatching has been shown to be temperature dependent (Wild, Chapter 16). However, we found a rather wide variation in the total integrated temperature for this event among the various crabs (sample size: seven), indicating little relationship between temperature and crab embryo development rates. It may be that something in addition to temperature (possibly photoperiod or diet) influences these rates.

ZOEAL STUDIES

Materials and Methods

Collecting and Handling

Larval hatching tanks received 20- μ m-filtered, UV-treated, ambient-temperature seawater at 1 to 2 liters/min. Initially, when crab larvae commenced to hatch, the seawater inlet valve was closed and aeration provided. Larvae were siphoned or dipped (using a 0.5-liter beaker) from the aquarium and concentrated in a container. Later in our studies, a screened container, partially immersed in seawater, was positioned beneath the aquarium water outlet to collect larvae. With this method, the seawater flow was not interrupted and the hatching tank did not receive supplemental aeration. With both methods, larvae were collected once daily after most had passed from the abbreviated prezoal stage (ca. 15 min) to zoal stage I.

Newly hatched crab zoeae received various treatments. Some were placed in 20- μ m-filtered seawater, counted, and distributed into cultures. Others were rinsed in 1- μ m-filtered, UV-treated seawater for varying time periods up to about 4 hr and then counted and distributed into cultures. Still other crab zoeae were concentrated in 1- μ m-filtered, UV-treated seawater, and treated with streptomycin sulfate (150 mg/liter) up to 24 hr as a prophylactic measure for bacterial suppression before being distributed into larval-culture systems.

Zoeal counts were made for all culture experiments. For flask culture experiments, zoeae were drawn by pipette, counted, then distributed into flasks. For mass-culture experiments, zoeae were siphoned with clear plastic tubing (about 5-mm od) directly into the cultures. They were counted as they were drawn into the tubing.

Culture Systems

Three methods for culturing zoeae were examined: (i) 250-ml flask cultures, (ii) large-scale mass cultures, and (iii) small-scale mass cultures.

Flask cultures. Flask experiments were conducted to identify suitable culture criteria for crab zoeae. Flask culture techniques were based on the studies of Reed (1969) and Gaumer (1971). We conducted a total of 44 flask experiments from 1972 through 1976; three 250-ml Erlenmeyer flasks were used in each experiment. Zoeae in 39 of these experiments were subjected to varying streptomycin-sulfate treatments and diets (Table 51). The five additional experiments were considered "controls"; i.e., the zoeae were not treated with streptomycin sulfate and were fed a diet of only brine shrimp nauplii (5-10/ml).

Large-scale mass cultures. We used four container types to test large-scale mass cultivation of zoeae during the 1971 to 1973 hatching seasons. These containers were all relatively large and differed in shape and construction material (Table 52).

TABLE 51. Culture Parameters Tested with Crab Zoeae in 250-ml Erlenmeyer Flasks, 1972-1976.

Culture parameters	Conditions
Seawater volume	200 ml
Zoal density	1/40 ml (5 larvae/flask)
Temperature	14 $\pm$ 1 C
Seawater filtration	1 μ m
Ultraviolet treatment	Low dosage (all flasks)
Streptomycin-sulfate treatment	No treatment
	Once weekly (150, 75, and 37 mg/liter)
	Thrice weekly (150, 75, and 37 mg/liter)
Water and food changes	Thrice weekly
Aeration	No aeration
Photoperiod	9-hr light/15-hr dark
Lighting type	Cool white fluorescent
Diet *	
Brine shrimp nauplii	No brine shrimp
	5-10/ml (unfed)
	5-10/ml (diatom or green algae-fed)
Rotifers (<i>Brachionus plicatilis</i>)	No rotifers
	25/ml
	50/ml
	100/ml
	150/ml
Diatoms (<i>Phaeodactylum tricornutum</i>)	No diatoms
	5 $\times$ 10 ⁴ /ml
	10 $\times$ 10 ⁴ /ml

* All diets in the flask cultures were presented either by themselves or in combination with brine shrimp nauplii.

TABLE 52. Large-scale Mass Culture Systems Used for Cultivation of Zoal-stage Larvae, 1971-1973.

Time period	Container code*	Culture volume (liters)	Container dimensions (cm) †			Container description
			length	width	depth	
1972-73	AB	315	64	64	81	Square with flat bottom; fiber-glassed wood; white epoxy finish.
1972-73	BV	800		107	104	Circular with concave bottom; fiberglass; blue gel-coat finish.
1971-73	WV	375		60	135	Circular with conical bottom; fiberglass; white gel-coat finish.
1971-73	BT	150	112	51	36	Oval (bathtub-shaped) with flat bottom; fiberglass; green gel-coat finish.

* Laboratory code series (in house) used to identify various container types.

† Inside dimensions to nearest cm.

Culture parameters varied widely among the various containers and between test runs with the same container. There was no "standard". Ambient-temperature seawater (ca. 11 to 15 C), filtered from 5 to 20 μ m and UV-treated, generally was used. Static water systems (with aeration and periodic water

exchanges) and flow-thru systems were both tested. Zoael stocking densities varied widely (from 5 to 125/liter). Brine shrimp nauplii were the standard diet, although other zooplankters and an alga were tested.

Small-scale mass cultures. Two basic substrate types, sand and screen, were employed in small-scale mass cultures (Table 53).

TABLE 53. Small-scale Mass Culture Systems Used for Cultivation of Zoael-stage Larvae 1974-1979.

Time period	Substrate type	Culture volume (liters)	Container dimensions (cm) *		Container description
			diameter	depth	
1974-76	Sand	9	25	30	Circular (bucket-shaped) Plastikan with flat, sand-covered bottom; polyethylene plastic; opaque white.
1976-79	Screen	8	20	30	PVC pipe section (green color) with Nitex screen bottom; held inside a Plastikan.

* Inside dimensions to nearest centimeter.

Sand. In 1974 we reduced the mass culture system size primarily for quality control and sought to optimize culture parameters (Table 54). The basic sand substrate system (22 cultures) had a thru-flow water mode. This system (Table 53) consisted of a commercially available, round, 15-liter, polyethylene plastic container (Plastikan: Container Supply Co., Garden Grove, CA) with a flat bottom. A layer of coarse sand, occasionally mixed with crushed oyster shell, covered the bottom to a depth of 10 to 13 cm. The sand covered a subsand filter constructed of 1.3-cm PVC pipe. The pipe was cross-shaped, perforated with 3.2-mm holes, and vented through the container wall to the outside where it was attached to a standpipe. Water depth inside the container was controlled by adjusting the height of the standpipe. The water inlet was situated just above and inside the culture container perimeter and was directed so as to provide a circular water current. During operation, water percolated down through the sand-oyster shell mix, passed through the subsand filter, and exited from the standpipe. Occasionally, an airstone was placed in the standpipe to create an airlift and facilitate water passage through the sand.

The sand-substrate system was modified into a recirculating water mode for three cultures. This was accomplished by placing an airstone in the standpipe and redirecting the water exiting from the standpipe back into the culture.

Screen. In early 1976, we developed a new small-scale mass culture method for zoael-stage larvae (Table 53) that represented a radical departure from previous approaches. This latest system, using a screen substrate, is the most satisfactory culture apparatus to date and we consider it our basic zoael culture system. We have used this system as described, or occasionally with minor design variations, for all subsequent experimentation.

TABLE 54. Culture Parameters Tested with Crab Zoeae in the Small-scale, Sand-substrate Containers, 1974-1976.

Culture parameters	Conditions
Culture volume	7 to 9 liters
Zoeal density	25/liter 50/liter 100/liter 139/liter
Temperature	Standard (14 ± 1 C) Ambient (10-15 C)
Seawater filtration	20 μ m
Ultraviolet treatment	Low dosage (all cultures)
Streptomycin-sulfate treatment	No treatment Initial treatment only (130 mg/liter) Once weekly treatment (130 and 150 mg/liter)
Seawater mode	Thru-flow (about 1.0 liter/min) Recirculating (via air lift)
Photoperiod	9-hr light/15-hr dark 24-hr light
Lighting type	Cool white fluorescent Blue filter (with cool white lamp)
Diet *	
Brine shrimp nauplii	5-10/ml 1-7/ml (variable)
Rotifers (<i>Brachionus plicatilis</i>)	No rotifers 11/ml 15/ml 1-3/ml (variable)
Diatoms (<i>Phaeodactylum tricornutum</i>)	No diatoms 5×10^4 /ml
Diatoms (<i>Thalassiosira pseudonana</i>)	No diatoms 5×10^3 /ml

* Rotifers and diatoms were always presented in combination with brine shrimp nauplii

The small-scale, screen-substrate apparatus consists of two plastic containers, one inside the other (Figure 112). Larvae are reared in the inner, screened-bottom container, while the outer container maintains water level and water passage from the system. The inner container consists of a 20-cm diameter PVC pipe section 33-cm long and fitted with a Nitex-screen bottom inserted 2.5 cm above the base. Water exit holes, 2-cm wide, are routed out just below the Nitex screening at about 2-cm intervals around the perimeter of the pipe section. The outer container is a Plastikan, 25-cm diameter by 30-cm high. Two holes are bored in the outer container, one in the center of the bottom, the other near the top. PVC pipe, 1.3-cm diameter, is plumbed between the two holes to facilitate equal water passage from the container. The container is positioned on a plastic supporting base to isolate the system from surrounding drain water. The water inlet is a glass tube (8-mm id) contoured and affixed to the inside wall of the inner container near the top. This provides a circular water flow directed slightly downward. Water flows into the inner chamber at the top, exists via the holes beneath the Nitex screening at the base, and then passes from the outer chamber (Plastikan) via the two interconnected drain pipes.

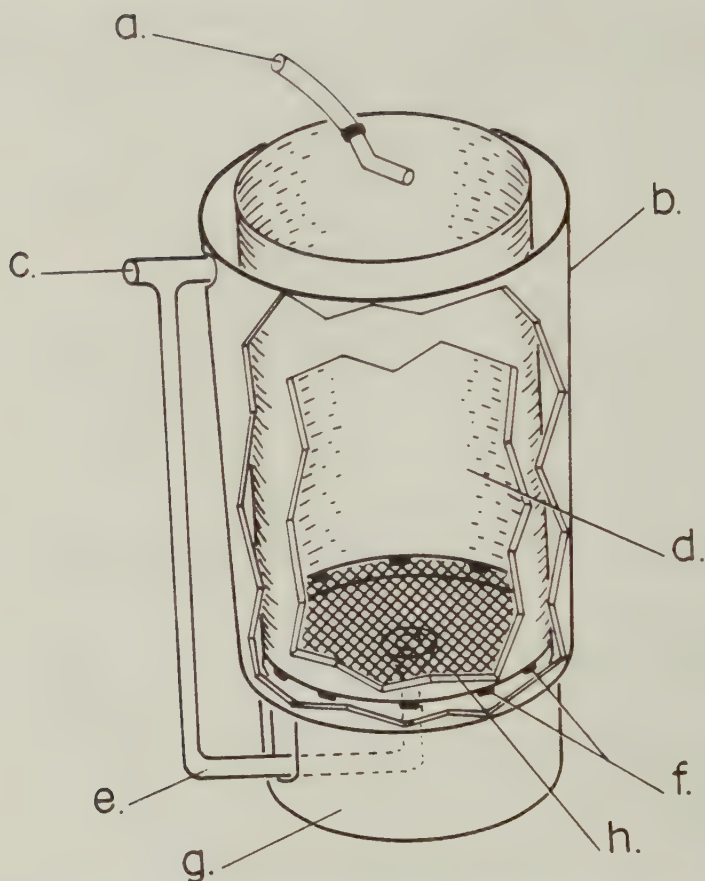


FIGURE 112. The screen-substrate culture apparatus used for crab zoeae; a, water inlet; b, outer culture chamber; c, water outlet—top; d, larval rearing chamber; e, water outlet—bottom; f, water exit ports from larval chamber; g, base support; h, Nitex screening.

Ten "standard" culture parameters were established based largely on previous experimentation. Screen substrate cultures were run using standard culture conditions and variations to these conditions (Table 55). All cultures were drained and cleaned approximately midway through the intermolt period of each zoeal stage (four cleanings per culture). Zoeae were first siphoned or pipetted into a tray and rinsed (two seawater exchanges). Counts were made of live and dead zoeae. Samples were routinely examined microscopically to confirm developmental stages and to determine, if possible, the cause of mortality. We estimated zoeal survivorship by stage. Megalopae were removed from the culture within 24 hr of achieving this stage because they cannibalize zoeae (Gaumer 1971). General observations were recorded daily on a standardized data sheet. These included culture temperature, larval behavior, developmental stage, percentage (estimated) of larvae at developmental stages, larval mortality, and culture-screen accumulations.

TABLE 55. Culture Parameters Tested with Crab Zoeae in the Small-scale, Screen-substrate Containers, 1976-1979.

<i>Culture parameters</i>	<i>Standard conditions</i>	<i>Variations</i>
Culture volume	7.9 liters	1.6 liters
Zoeal density	100/liter	200/liter
Temperature	14 $\pm$ 1 C	17 $\pm$ 1 C
Water filtration	3 μ m	1 μ m
		20 μ m
Streptomycin-sulfate treatment	None	150 mg/liter (8-hr initial treatment)
		150 mg/liter (21-hr initial treatment)
Screen mesh size	90 μ m	153 μ m
Photoperiod	9-hr light/15-hr dark	24-hr light (continuous)
		24-hr dark (continuous)
Lighting type	Cool white fluorescent	Full spectrum fluorescent (580 and 465 M μ)*
		Chroma-50 fluorescent (500 M μ) †
		Blue filter (with chroma-50 lamps) ‡
Diet		No variations
Brine shrimp nauplii	5-10/ml	No variations
Water flow rate	0.5-0.8 liters/min	

* Spectra-lite Co., Holiday, Florida

† Acrylite 668-0 blue; American Cyanamid Co.

‡ General Electric Co.

Mean sizes of zoeae hatched in screen-substrate containers in 1977 and 1979 were compared with mean sizes of preserved zoeae captured from the Gulf of the Farallones in 1977 (Reilly, Chapter 6). The laboratory-hatched zoeae were reared using standard culture conditions (Table 55). Total lengths were measured from the tip of the dorsal spine to the tip of the rostral spine. The female parent origins of the laboratory-hatched 1977 zoeae were not recorded. The laboratory-hatched 1979 zoeae were from a female that was captured in the Gulf of the Farallones in July 1978, spawned in the laboratory in October 1978, and whose eggs hatched in January 1979.

Results

Collecting and Handling

A screened container positioned beneath an aquarium overflow, and partially immersed in seawater, proved best for larval collection. With this method only swimming larvae were collected and water quality was better in hatching tanks with continuous water flows. When the water in hatching tanks was left static overnight with aeration, the water quality deteriorated as live and dead larvae, empty egg cases, and debris accumulated and became mixed. A larval rinse in 1- μ m-filtered, UV-treated seawater, after collection, appeared to be a good sanitary procedure, although statistical evidence to support its value is lacking. Subjecting zoeae to an initial treatment of streptomycin sulfate had no influence on zoeal survival during culture experiments. This procedure was used only briefly. A pipette was satisfactory for collecting and counting small numbers of zoeae for flask cultures. Relatively large numbers of zoeae were expediently collected, counted, and distributed into culture systems by siphoning with clear plastic tubing.

Culture Systems

Flask cultures. Zoeae cultured in 250-ml flasks generally showed very poor survival. In the five "control" experiments (15 flasks), mortalities were low during the first three zoeal stages, then progressively increased to total mortality by the megalopal stage. Only one "control" zoea reached the megalopal stage.

Survival in flask-cultures of zoeae treated with streptomycin sulfate occasionally was more successful than non-treated zoeae. Of eight experiments (24 flasks) which were presented varying treatments of this antibiotic (Table 51), and in which larvae were fed a diet of only brine shrimp nauplii, two zoeae (from one experiment) reached the megalopal stage. Antibiotic dosage (150, 75, or 37 mg/liter) or frequency of treatment (once or thrice weekly) had no correlation with culture success.

Zoeae cultured in flasks without streptomycin often were infected with the epibiotic, filamentous bacterium *Leucothrix mucor*. This bacterium usually appeared about day 14 and, by day 28, bacterial growth was heavy and encumbered larval movement. No zoeae in the streptomycin-treated cultures had this filamentous bacterium. However, elimination of this bacterium did not improve zoeal survival.

Many streptomycin-treated zoeae showed developmental abnormalities. These larvae frequently skipped zoeal stage V and died while molting from stage IV to the megalopal stage, or while molting to an abnormal combination of stage V and megalopa (we dubbed these "five-a-lopae"). No "five-a-lopae" survived. No abnormal larvae were found in untreated cultures.

Flask-cultured zoeae presented varied diets (Table 51) did not show improved survival over zoeae presented only brine shrimp nauplii. The rotifer *B. plicatilis*, either by itself or in combination with brine shrimp nauplii, did not improve zoeal survival. The addition of the diatom *P. tricornutum* to cultures did not improve zoeal survival. Some brine shrimp nauplii were fed a diatom diet and then fed to zoeae. This also did not help zoeal survival. A diet of brine shrimp nauplii which had been fed the green alga *Tetraselmis* sp. resulted in heavy zoeal mortality. Unfed zoeae (starvation diet) usually showed total mortality before completing the molt to stage II.

Only one of the 44 flask experiments was relatively successful. Larvae used in this experiment hatched in 1975 from an ovigerous female shipped to MCL from Washington state. Survival was 27% (four larvae) to the megalopal stage; however, these four megalopae appeared unhealthy and none completed the molt to the first crab instar. Throughout this experiment, the larvae were treated with streptomycin sulfate (150 mg/liter) thrice weekly and fed a combination diet of brine shrimp nauplii (5/ml), rotifers (50/ml), and diatoms (10×10^4 /ml). Attempts to repeat these results were unsuccessful.

Large-Scale Mass Cultures. The four container types used to test large-scale mass cultivation feasibility during the 1971 to 1973 larval-hatching seasons (Table 52) generally proved unsuccessful.

Four experimental trials were made with the AB container. Two trials were conducted at ambient seawater temperature (13–14 C), one with a static water mode, the other thru-flow (6 liters/min). Zoeae were stocked at about 8 to 11/liter. Brine shrimp nauplii were supplied at a low concentration for the thru-flow trial (56/liter), while the zoeae in the static culture were unfed. Zoeal mortality in both cultures was high; the unfed culture was suspended after 6 days and the fed culture after 14 days. Few live zoeae remained. The remaining two trials with the AB tank were conducted at an elevated temperature (15.7–16.8 C) and both were thru-flow (6 liters/min). Zoeae were stocked at about 10/liter. A small amount of brine shrimp nauplii was supplied to one culture while zoeae in the other culture were unfed. Both cultures were terminated within 1 week due to high mortalities.

One experimental trial was made with the BV container. This trial used ambient-temperature (13.5 C) seawater with a thru-flow mode. Zoeae were stocked at 125/liter and supplied with brine shrimp nauplii (0.5/ml). Zoeal mortality was observed early, rapidly increased, and the experiment was discontinued after 10 days with total mortality.

One experimental trial was made with the WV container. This trial was conducted in a static seawater mode at a salinity of 30 ppt and temperatures which varied from 13.8 to 16.7 C. A sulfa drug (sodium sulfamethazine, 30 mg/liter) was added. A total of 2,000 zoeae (about 5/liter) was stocked and fed brine shrimp nauplii (27/liter). Zoeal survivorship appeared to be good for the

first few days; however, by day 6, accumulations of dead zoeae were noted and high mortality ensued shortly thereafter. The culture was terminated after 10 days with only two live zoeae remaining.

One experimental trial was made with the BT container. This was conducted at ambient temperature (11.4–17.5 C) with 5- μ m-filtered, aerated seawater that was changed every 2, 3, or 4 days. A total of 2,000 zoeae (about 13/liter) was stocked. Zoal forage, added after each water change, consisted of brine shrimp nauplii (ranging from 67 to 267/liter per feeding), echiuroid worm *Urechis caupo* larvae, (ranging from 0.07 to 3.3/ml), and a diatom *Phaeodactylum tricornutum* at a concentration of 2×10^4 cells/ml. Zoal survivorship after 30 days was about 8% and declined to about 2% by day 60. A total of six zoeae (0.3%) subsequently molted to the megalopal stage.

Small-scale mass cultures. Results were gathered and evaluated for both the sand and screen substrates.

Sand. Twenty-five sand-substrate cultures were evaluated during three hatching seasons (1974–1976). Flooding was a major problem with most of the 22 thru-flow cultures. This was caused by sand clogging the drain pipe openings. Swiveling of the standpipe to a lower angle failed to compensate for the flooding problem. An airstone placed in the standpipe helped alleviate flooding but made it difficult to regulate the culture water level. This resulted from a variable "pulling" of water through the sand in response to the degree of sand-clogging of the drain pipe openings. Generally, sand-clogging of the drain pipes progressively increased.

Recirculation of the water in the sand-substrate culture system (three cultures) eliminated the flooding but presented additional problems. The sand harbored organisms such as nematodes and copepods. Dead larvae and excess forage which accumulated on the sand were difficult to see and remove. Consequently, essential sanitary procedures could not be followed.

Mean culture success with the 22 thru-flow containers was about 4% to the megalopal stage (Table 56). Mortality was highest during the initial zoeal stages and in 11 cultures total mortality occurred prior to the megalopal stage. Five thru-flow sand cultures (23%) were infected with the fungus *Lagenidium* sp. The fungal infection generally appeared by the second zoeal stage and resulted in extensive, if not total, zoeal mortality. Also, zoeal spine breakage, particularly the dorsal spine, was common in most cultures. Stage III larvae, which were noted to be sensitive to sudden lighting changes, darted about and impacted sharply with culture walls apparently resulting in spine breakage. These hollow, broken spines also served as an entry portal for ciliate protozoans that frequently were seen passing through the break into the live but weakened larvae. Most zoeal mortalities, excluding those caused by the fungus *Lagenidium* sp., had broken dorsal spines.

The most successful sand-substrate culture started with 175 (25/liter) newly hatched zoeae in a thru-flow system (1 liter/min) maintained at 14 ± 1 C. The diet was newly-hatched brine shrimp nauplii (5/ml), rotifers *B. plicatilis* (15/ml), and diatoms *P. tricornutum* (5×10^4 /ml), all added daily. Diatom feeding was terminated on day 26. Unidentified copepods, nematodes, and diatoms also became established in the culture. Streptomycin sulfate (150 mg/liter) was added once weekly, although this was a thru-flow system. At day 30, zoeal

TABLE 56. Relationship Between Parent Origin, Egg Mass, and Survival with the Fungus *Lagenidium* sp. Data are from 72 Small-scale Mass Cultures, 1974-1979.

Female parent origin	Egg mass		Date of larval hatch	Culture substrate	Observance of fungus	Survival to megalopa (%)
	Location of spawn	No. days in MCL water				
AK *	AK	26	06/04/76	sand screen screen screen screen screen screen screen	yes yes yes yes yes yes no no	14 16 12 9 9 9 24 1
WA †	WA	8	03/23/76	sand sand sand screen screen screen screen screen screen	no no no yes yes no no no no	0 0 0 3 0 12 9 9 7
WA ‡	WA	2	03/03/77	screen screen screen screen screen screen screen screen screen screen screen screen screen	no no no no no no no no no no no no no	81 67 57 53 40 33 32 29 24 23 17 16
CC §	CC	4	01/28/74	sand sand sand sand	no no no no	0 0 0 0
EU 	EU	1	02/17/75	sand	no	37
EU ¶	EU	6	12/23/76	screen	no	33
RR *	RR	1	01/29/76	sand sand sand sand sand sand sand sand screen screen screen screen screen	yes yes no no no no no no yes no no no no	0 0 7 6 5 3 1 0 0 0 0 0 0

TABLE 56. (Continued)

Female parent origin	Egg mass		Date of larval hatch	Culture substrate	Obser- vance of fungus	Survival to megalopa (%)
	Location of spawn	No. days MCL in water				
EU **	MCL	91	02/06/78	screen	no	12
				screen	no	10
				screen	no	1
				screen	no	0
				screen	no	0
				screen	no	0
RR ††	MCL	119	04/04/76	sand	yes	0
				sand	yes	0
				sand	no	3
				sand	no	2
				sand	no	1
RR ††	MCL	70	01/03/77	screen	yes	25
				screen	yes	22
				screen	yes	13
				screen	yes	1
				screen	yes	0
				screen	yes	0
RR §§	MCL	61	01/14/78	screen	yes	0
				screen	yes	0
				screen	yes	0
				screen	yes	0
				screen	yes	0
				screen	yes	0
SF †† †	MCL	85	01/17/79	screen	yes	0
				screen	no	0

* Ovigerous female collected in May 1976 at Auk Bay, Alaska.

† Ovigerous female collected in March 1976 by NMFS personnel, Manchester, Washington.

‡ Ovigerous female collected in March 1977 in waters off Washington State and transported to MCL via Bodega Marine Laboratory.

§ Ovigerous female collected in January 1974 near Crescent City, northern California.

|| Ovigerous female collected in February 1975 near Eureka (off the entrance to Humboldt Bay), northern California.

¶ Ovigerous female collected in July 1976 near Eureka.

Ovigerous female collected in January 1976 off the mouth of the Russian River, central California.

** Collected in November 1977 near Eureka, California. This female spawned in the laboratory on 11/07/77.

†† Collected in June 1974 as a megalopa off the mouth of the Russian River. This female gave larvae for experiments in 1976 and 1977.

§§ Collected in June 1974 as a megalopa off the mouth of the Russian River. This female gave larvae for only one set of experiments (1978).

||| Collected in June 1978 near San Francisco (Gulf of the Farallones). This female spawned in the laboratory on 10/23/78.

stage-III exuviae were common on the sand surface. The first stage V zoeae were observed 3 days later. Most of the zoeae had developed to stage V by day 41 and the first megalopa was recorded on day 47. On day 62, a total of 64 megalopae (37% survival) were counted (Table 56).

Screen. Fifty screen substrate cultures were evaluated from 1976 through 1979. Results of the initial (1976) cultures largely were inconclusive. The 18 cultures conducted in 1977 represent our most intensive series to evaluate this apparatus. These cultures were conducted in pairs and results are presented as nine duplicate-culture trials (Tables 57 through 60). Evaluations of most culture parameters are based on these 18 cultures.

TABLE 57. Culture Conditions for Crab Zoeae in Nine Duplicate-culture Trials during 1977.

Trial number	Female parent origin	Larval density (no./liter)	Temp. ($\pm 1^{\circ}$)	Water filtration (μ m)	Lighting		Initial streptomycin-sulfate treatment (150 mg/liter)	Culture screen size (μ m)
					Photoperiod (hr)	Type		
1*	RR†	100	14	3	9	FS†	8 hr	90
2*	RR	100	14	3	9	F§	0	90
3*	RR	200	14	3	9	FS	8 hr	90
4.	WA	100	14	3	9	FS	0	90
5.	WA	100	14	3	9	FS	0	90
6.	WA	200	14	3	9	FS	0	90
7.	WA	100	17	20	9	FS	0	153
8.	WA	100	14	1	24	F	0	90
9.	WA	100	14	3	24	F	0	90

* Denotes presence of fungus *Legionidium* sp.

† Collected as megalopa off the mouth of the Russian River, central California, cultivated to maturity and mated in the laboratory

|| Washington State.

‡ Fluorescent, full spectrum lamps (Specto-lite Co., Holiday, FL).

§ Fluorescent, cool white lamps.

TABLE 58. Survivorship at Each Larval Stage in Nine Duplicate-culture Trials Completed during 1977.

Trial no.	Stage and survivorship											
	I		II		III		IV		V		Megalopa	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1a *	790	100	325	41.1	186	23.5	2	0.2	- discontinued -			
b *	790	100	433	54.1	394	49.9	279	35.3	211	26.7	174	22.0
2a *	770	100	288	37.4	271	35.2	198	25.7	20	2.6	3	0.4
b *	770	100	302	39.2	281	36.5	263	34.2	217	28.2	191	24.8
3a *	1580	100	637	40.3	555	35.1	407	25.8	232	14.6	210	13.3
b *	1580	100	659	41.7	553	35.0	28	1.8	1	0.1	-	-
4a	790	100	702	88.2	675	85.4	613	77.6	281	35.8	178	22.5
b	790	100	715	90.5	705	89.2	645	81.6	396	50.1	299	29.0
5a	790	100	730	92.4	712	90.1	688	87.1	612	77.5	420	53.2
b	790	100	738	93.4	727	92.0	689	87.2	620	78.5	448	56.7
6a	1540	100	1462	94.9	1415	91.9	1130	73.4	657	42.7	259	16.8
b	1540	100	1448	94.0	1445	93.8	1337	86.8	520	33.8	252	16.4
7a	780	100	778	99.7	no counts				750	96.9	629	80.6
b	777	100	670	86.2	no counts				617	79.4	520	66.9
8a	250	100	210	84.0	204	81.6	182	72.8	140	56.0	101	40.0
b	250	100	205	82.0	193	77.2	165	66.0	102	40.8	83	33.2
9a	250	100	213	85.2	210	84.0	168	67.2	120	48.0	79	31.6
b	250	100	206	82.4	200	80.0	166	66.4	100	40.0	61	24.4

* Denotes presence of fungus *Lagenidium* sp.**TABLE 59. Development Rates of Crab Zoeae in Nine Duplicate-culture Trials during 1977.**

Trial number	Zoeal stage and intermolt period* (days)				
	I	II	III	IV	V
1a	8	8	12	-	-
b	8	7	9	9	12
2a	8	8	8	10	13
b	8	8	8	9	13
3a	8	8	8	10	12
b	8	8	9	11	-
4a	8	7	8	11	12
b	8	7	6	12	12
5a	7	8	7	10	13
b	7	7	8	9	14
6a	7	8	7	10	13
b	7	7	6	11	14
7a	5	8	3	7	8
b	5	8	3	7	8
8a	8	7	8	10	13
b	8	7	8	11	13
9a	8	7	9	10	13
b	8	7	10	9	15

* Intermolt period measured from the day that larval molting to a stage commences up to, but not including, the day that larval molting to the next stage ensues.

TABLE 60. Calculated Number of Brine Shrimp Nauplii Provided to Crab Zoeae in Nine Duplicate-culture Trials during 1977.

Trial number	Nauplii/zoeae/day by stage				
	I	II	III	IV	V
1a	25.0	44.2	51.5	nd *	nd
b	25.0	29.1	26.4	43.8	49.3
2a	nd	nd	nd	nd	nd
b	nd	nd	nd	nd	nd
3a	17.7	22.6	25.0	19.7	71.5
b	25.5	18.0	16.7	nd	nd
4a	9.2	12.6	13.1	25.2	78.6
b	8.5	12.7	17.7	23.0	47.3
5a	15.1	17.0	18.6	22.8	40.2
b	14.0	20.3	20.2	22.0	40.9
6a	8.0	10.2	14.6	20.4	43.8
b	8.0	13.1	14.0	17.4	58.4
7a	34.2	48.7	114.7	128.9	151.4
b	33.7	54.0	97.9	102.0	139.9
8a	5.7	9.8	12.3	20.3	38.5
b	5.3	9.3	13.0	20.4	57.3
9a	6.0	6.7	10.6	20.8	48.7
b	6.0	9.7	13.0	20.7	58.6
Mean	13.0	21.1	30.0	36.2	66.0

* No data

Reducing the container size and culture volume from the "standard" 7.9 liters to 1.6 liters had no apparent effect on culture success. The smaller cultures (four) averaged 33% survival to the megalopal stage (range 24 to 40%) (Table 58, trials 8 and 9).

Larval survival in nonfungal-infested cultures (Figure 113) averaged about 40% (range 16 to 81%). Larval survival to zoeal stage IV in the high-density cultures (200/liter) compared favorably with those of standard density (100/liter) in the absence of *Lagenidium* sp. However, a sharp mortality increase occurred in the high-density cultures between zoeal stages IV and V (Figure 114).

The average water temperature for each culture remained within planned limits. However, day-to-day temperature fluctuations, at times, exceeded planned limits (± 1 C). The maximum extreme beyond design limits was 4.2 C, but this was corrected within 18 hr. Morning temperatures averaged slightly less than afternoon temperatures.

Zoeae cultured at an elevated temperature (17 C) in 1977 (Table 57) had significantly shorter intermolt periods (Table 59, trial 7) than zoeae cultured at the standard temperature (14 C). The zoeae cultured at elevated temperature took only 31 days overall, an average of 15 days less to attain the megalopal stage (Figure 115). These cultures also had the best larval survival to the megalopal stage (74%), a figure significantly greater than that of standard-temperature cultures (Figure 116).

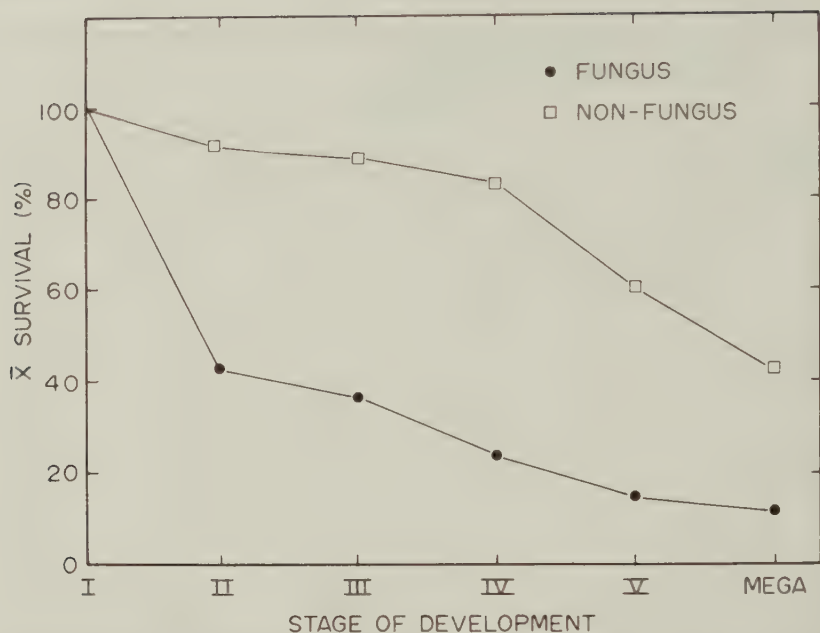


FIGURE 113. Comparative larval survivorship between fungal-infected cultures (trials 1 and 2) and non-fungal-infected cultures (trials 5, 8, and 9). Data from high-density and elevated-temperature cultures not included.

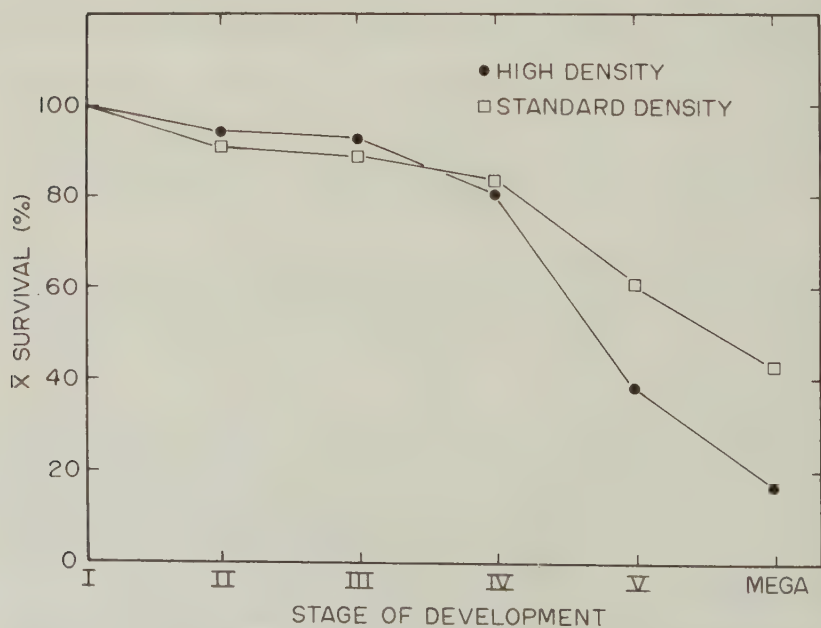


FIGURE 114. Comparative larval survivorship between standard-density (100/liter) cultures (trials 5, 8, and 9) and high-density (200/liter) cultures (trial 6). Data from fungal-infected and elevated-temperature cultures not included.

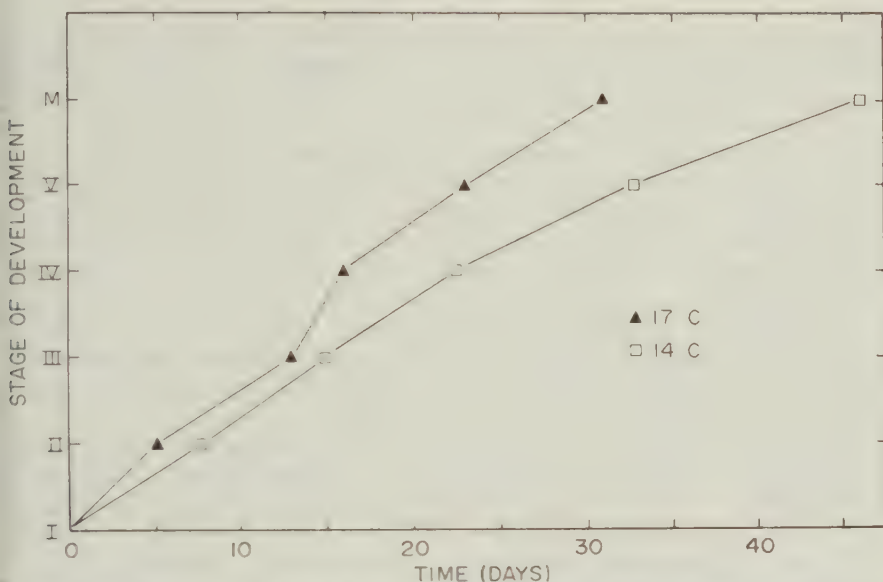


FIGURE 115. Comparative larval development rates between standard-temperature (14 C) cultures (trials 5, 8, and 9) and elevated-temperature (17 C) cultures (trial 7). Data from fungal-infected and high-density cultures not included.

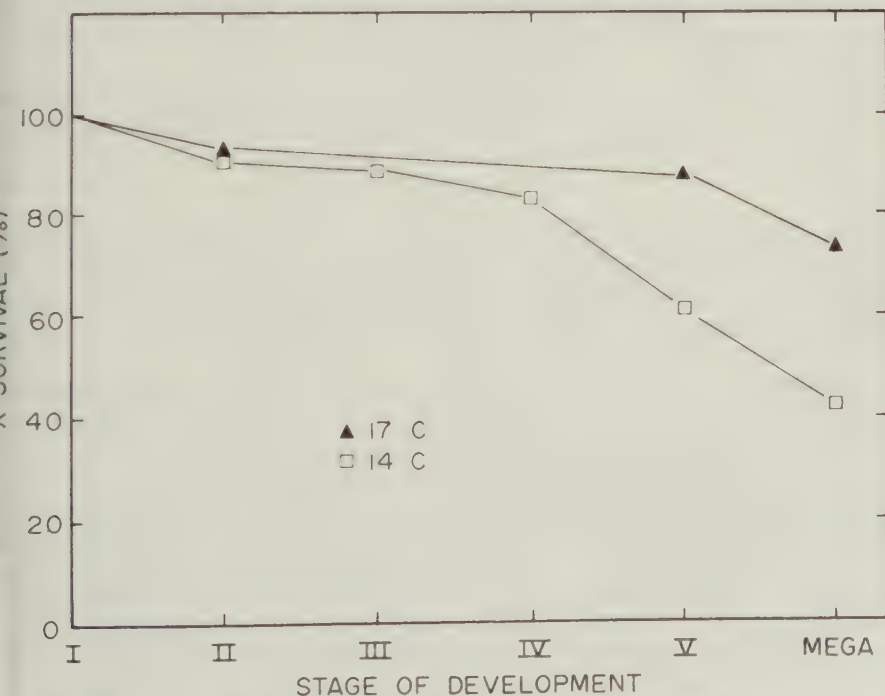


FIGURE 116. Comparative larval survivorship between standard-temperature (14 C) cultures (trials 5, 8, and 9) and elevated-temperature (17 C) cultures (trial 7). Data from fungal-infected and high-density cultures not included.

Unfiltered seawater proved unsatisfactory because culture screens became clogged and resulted in flooding. Coarser screen-mesh sizes ($153\text{ }\mu\text{m}$) could not be used to alleviate this problem because newly hatched brine shrimp nauplii passed through the mesh. The three seawater filtration levels we tested (1, 3, and $20\text{ }\mu\text{m}$) resulted in fair to good culture success (Tables 57 and 58). Larval survival was slightly better in the $1\text{-}\mu\text{m}$ -filtered seawater when compared to the $3\text{-}\mu\text{m}$ -filtered seawater for cultures that had a 24-hr photoperiod (trials 8 and 9, respectively). The $20\text{-}\mu\text{m}$ -filtered seawater could not be compared to the others because temperature, photoperiod, and screen-mesh size differed at this filtration level.

Initial treatment of zoeae with streptomycin for 8 or 21 hr had no discernible effect on larval survival. Routine examinations of these zoeae revealed no filamentous bacteria and no abnormal development. Untreated control larvae also showed no epibiotic bacteria or abnormalities.

The $90\text{-}\mu\text{m}$ screen mesh accumulated more debris than the $153\text{-}\mu\text{m}$ screen, but there was no evidence that this adversely affected larvae. Sanitary procedures applied at each developmental stage apparently prevented accumulated debris from contaminating the larvae. Also, there was no evidence that either of the screen sizes caused larval spine damage through entrapment.

Continuous 24-hr light or 24-hr dark photoperiods, when compared to a 9-hr light/15-hr dark cycle, disclosed no discernible differences for larval development rates, survivorship, or forage requirements. Beyond stage III, zoeae were particularly sensitive to sudden lighting changes which resulted in increased zoeal activity and spine breakage. This behavior was similar to that noted in sand substrate cultures.

The four types of illumination (Table 55) had little noticeable effect on zoeal activity, survivorship, or development. The blue filter was used to simulate ocean conditions at a depth of 10 m. Light passing through this filter was the least intense of the four lighting types and occasionally seemed to reduce zoeal activity.

Daily aliquot sampling with a 1-ml pipette revealed that brine shrimp nauplii densities in screen-substrate cultures varied greatly. Day-to-day densities in all screen cultures examined averaged between 5 and 10 nauplii/ml (range 0 to 26/ml). The average number of brine shrimp nauplii required for successive developmental stages increased progressively (Table 60).

A water-flow rate of 0.5 to 0.8 liters/min, adjusted daily, appeared adequate for zoeal culture. This rate resulted in a complete turnover of seawater in a 7.9-liter container every 16 min.

Intermolt periods for zoeae in the eight pairs of standard-temperature trials in 1977 were fairly uniform for the first two developmental stages, but varied at subsequent stages. They took from 7 to 8 days to achieve stage II and approximately the same length of time to achieve stage III. Stage III averaged 8.2 days (range 6 to 12 days); stage IV, 10.1 days (range 9 to 12 days); and stage V, 13.0 days (range 12 to 15 days). Overall, zoeae averaged 46 days (range 45 to 49 days) in standard-temperature cultures to achieve the megalopal stage (Table 59).

The 50 screen substrate cultures showed a mean survival of 14% (range 0 to 81%). Survival in the 28 cultures not infected with fungus averaged about 21%. The 22 cultures (44%) infected with *Lagenidium* sp. showed a mean survival of only 5% (Table 56).

Overall survival to the megalopal stage for the nine duplicate-culture trials conducted in 1977 averaged about 30% (range 0 to 81%; Table 58). Survival in the three trials (trials 5, 8, and 9) cultured under standard conditions, and not infected with fungus, averaged about 40% (range 28 to 55%). In these, survival was very good to stage III, began to decrease by stage IV, and further declined during stage V and during metamorphosis to the megalopal stage.

The three duplicate-culture trials infected with *Lagenidium* sp. (trials 1, 2, and 3) revealed that the fungus generally appeared by zoeal stage II and persisted from 1 to 3 or more weeks. The infection had a varying effect on zoeae. In some cultures total mortality occurred by zoeal stages IV and V; however, in other cultures mortality was slight and then, apparently disappeared completely by zoeal stage V. Survival in the two fungal-infected trials (1 and 2), cultured under standard conditions, averaged about 12% (range 0 to 25%) (Table 58; Figure 113).

Laboratory-hatched 1977 and 1979 zoeae were smaller than field-caught 1977 zoeae (Table 61). The mean size differences were negligible at stage I, but grew progressively greater as zoeae developed to stage V. At stage V, the laboratory-hatched 1977 zoeae were 29% smaller than field-caught 1977 zoeae. The difference in mean sizes was not as great with laboratory-hatched 1979 zoeae compared with field-caught 1977 zoeae. These were almost identical at stages I through III. By Stage V, laboratory-hatched 1979 zoeae averaged only 12% smaller than field-caught 1977 zoeae. Also, laboratory-hatched 1977 zoeae were significantly smaller than laboratory-hatched 1979 zoeae.

Discussion

Using flask experiments, we were unable to identify suitable culture criteria for crab zoeae. Not only were we unable to duplicate the relatively successful results of Reed (1969) and Gaumer (1971), but results of our experiments with antibiotics (streptomycin sulfate) and diets (brine shrimp, rotifers, and algae), although variable, generally showed little or no beneficial effect on zoeal survival.

Our antibiotic experiments in flasks showed that streptomycin sulfate likely caused developmental abnormalities. Also, even though the antibiotic eliminated filamentous bacteria, zoeal survival was not consistently improved. On the basis of these observations, the use of streptomycin sulfate with flask-cultured zoeae is of doubtful benefit. However, other antibiotics possibly would improve survivorship. Poole (1966) was able to bring crab larvae to the megalopal stage in static-water cultures treated with a mixture of streptomycin sulfate (132 mg/liter) and penicillin (8 mg/liter). Survivorship in these cultures is unknown. Fisher and Nelson (1978), also working with static-water cultures, obtained 91% survival to the megalopal stage with chloramphenicol (5 mg/liter), 84% with a mixture of streptomycin sulfate (100 mg/liter) and penicillin-G (100 mg/liter), and 51% with untreated control zoeae.

TABLE 61. Sizes of Field-caught (1977) and Laboratory-hatched (1977 and 1979) Dungeness Crab Larvae.

Larval stage	Type of measurement	Field-caught larvae				Laboratory-hatched larvae							
		1977*				1977*				1979			
		No. measured	Mean (mm)	Range (mm)	No. measured	Mean (mm)	Range (mm)	No. measured	Mean (mm)	Range (mm)			
I	Length †	34	2.05	1.91-2.16	20	2.06	1.96-2.18	20	2.05	1.93-2.19			
II	Length.....	23	2.87	2.67-3.19	20	2.72	2.60-2.84	14	2.86	2.73-3.12			
III	Length.....	9	4.31	3.90-4.61	5	3.84	3.72-3.91	13	4.03	3.70-4.25			
IV	Length.....	7	6.89	6.76-7.06	6	5.44	5.34-5.54	12	6.29	5.55-6.43			
V	Length.....	4	9.69	9.22-10.10	2	6.89	6.86-6.91	8	8.49	7.70-8.85			
Megalopa	Length †	50	6.67	6.01-7.15	8	4.70	4.33-5.00	10	5.14	4.93-5.52			
	Width §	50	4.07	3.31-4.70	8	2.82	2.65-3.14	10	3.04	2.83-3.25			

* Measured by Paul N. Reilly, Calif. Dept. Fish and Game, Menlo Park, CA.

† Zoal length = distance from tip of dorsal spine to the tip of rostral spine.

‡ Megalopal length = distance from back of carapace (excluding dorsal spine) to tip of rostral spine.

§ Megalopal width = greatest width of carapace.

Our diet experiments were inconclusive because both the "control" and the combination diets resulted in poor zoeal survival. One combination diet looked promising with 27% survival to the megalopal stage and, occasionally, the "control" diet looked promising. However, we were unable to duplicate these results.

Reasons for poor survival of zoeae in flask experiments are not fully understood. Factors other than diet or bacterial pathogens probably are responsible for the mortalities. Most flask experiments were conducted before we were "fungus conscious"; therefore, we do not know whether *Lagenidium* sp. infected these zoeal cultures. It is unclear whether zoeal survival was a function of zoeal vigor, parental stock, or the culture conditions to which zoeae were subjected. We eventually abandoned flask experiments and concentrated our efforts on larger systems.

The large-scale cultures also proved unsuccessful. It became evident during the early phases of these experiments that culture parameters could not be controlled adequately. Culture temperatures were highly erratic and feeding regimens were poor with respect to frequency, ration, and, at times, quality.

Zoeal culture success in smaller-scale sand substrate containers, although better than the large-scale cultures, also was poor. This performance could be traced to mechanical problems that frequently resulted in flooding and to contaminants that thrived in the sand substrate. Recirculation of water (three cultures) served to elucidate the sand substrate contamination problem. The mechanical culture problems could have been resolved, but the sand substrate contamination problem prompted us to abandon this culture method.

The screen-substrate apparatus, with a thru-flow water mode, was reasonably successful. Inconsistencies in results (variable survivorship rates) were due principally to the fungus *Lagenidium* sp. It is not clear how the fungus entered the cultures. Three possible sources were considered: (i) via the incoming seawater, (ii) from the female parent crab, or (iii) from the brine shrimp nauplii.

Lagenidium sp. is indigenous to bays and estuaries (Armstrong et al. 1976); and, because it has been observed on Dungeness crab eggs (Armstrong and Fisher 1977), it is likely that the fungus occurs in open coastal waters. Spores of *Lagenidium* sp. measure $7 \times 5 \mu\text{m}$ (Armstrong et al. 1976). Most zoeal experiments at MCL were conducted with 3- μm -filtered seawater that originated from the open coast (Ebert et al. 1974). Because this filter rating is not absolute, it is likely that larger particles, possibly the size of fungal spores, could have entered our zoeal cultures.

Lagenidium sp. in zoeal cultures may originate directly from the female parent crab. Armstrong and Fisher (1977) found that *Lagenidium* sp. generally covered 5 to 10% of the total egg mass of Dungeness crabs. We also observed the fungus on egg masses. It is possible that zoeae are mildly infected upon hatching and, if so, fungal spores could encyst on zoeal exoskeletons or immediately achieve germ-tube penetration. In either instance, the zoeae could be active swimmers and appear outwardly healthy. Armstrong et al. (1976) speculate that fungal germ-tube penetration probably occurred at ecdysis while the zoeal exoskeleton was still soft. This could account for the typical fungal-induced zoeal mortality that we observed at stage II. Also, in those instances where fungal-induced mortality was evident at stage I, the germ-tube penetration could have occurred during the molt from prezoae to stage I.

Fungal infection of zoeae was directly correlated with the amount of time egg masses were held in the laboratory. Zoeae in the small-scale mass culture experiments from 1974 through 1979 originated from 11 different female crabs. Seven of these females were captured and transported to the laboratory while bearing egg masses (ovigerous). Eggs on most of these crabs spent a relatively short period of time (< 26 days) in MCL water before hatching larvae (Table 56). The other four females were brought to the laboratory before egg extrusion spawned their egg masses in the laboratory, and the eggs remained in MCL water for their entire incubation period. Thirty-three cultures were established with zoeae that hatched from eggs held in MCL water 26 days or more. Of these cultures, about 64% had fungal infections. The other 39 cultures had been in MCL water less than 26 days and showed only about 15% infection. The temperature (ambient or refrigerated) of seawater holding ovigerous females had no apparent effect on the occurrence of fungal infection.

These observations point out that, to minimize fouling of egg masses by fungus or other pathogens and subsequent infection of zoeae, close attention should be given to the collecting, transporting, and holding of ovigerous females. Optimum laboratory conditions for holding these females include an abundant flow of UV-treated, 1- μ m-filtered seawater, and a sand substrate that will help cleanse and protect egg masses during the incubation period. Fisher (1976) and Fisher and Nelson (1977) report that treating Dungeness crab eggs with the chemotherapeutic malachite green (1 ppm, 3 times/week) reduced filamentous fouling and egg mortalities. Perhaps a prophylactic treatment of egg masses with malachite green would also reduce fungal infection of crab zoeae.

The third possible source of *Lagenidium* sp. in zoeal cultures is brine shrimp nauplii. The surfaces of brine shrimp cysts often harbor contaminants. We do not know, however, if any of these are fungal in nature. If *Lagenidium* sp. exists on cyst surfaces, it is possible that it could be transferred to zoeal cultures, especially when cysts were hatched by our original (prior to 1979) method of incubating cysts in 25 C seawater for 48 hr. Nauplii obtained by this method were washed thoroughly with UV-treated, 1- μ m-filtered seawater before feeding to zoeae. This procedure should eliminate most free-swimming spores, although it would not remove the fungus from nauplii that had already been infected. Our more recent method of decapsulating cysts utilized the chlorine technique (Sorgeloos et al. 1977). This treatment undoubtedly would have destroyed any exobiotic fungus of the cysts and thereby prevented the nauplii from being infected. However, zoeae fed with these nauplii were also infected with *Lagenidium* sp. Therefore, it is unlikely that the fungus was introduced to our zoeal cultures via brine shrimp nauplii.

Generally, the various culture parameters to which zoeae were subjected (Tables 54, 55, and 57) had little effect on the initial occurrence of fungal infection. Both high-density, and elevated-temperature cultures showed variable degrees of infection; some were seriously infected and others showed no fungal infection. One parameter, the rate of water flow into the screen substrate containers, appeared to have an effect on the degree of infection. Once the fungus appeared in a culture, water flow was increased from about 0.5 to 0.8 liters/min. This occasionally resulted in abatement of the larval mycosis.

Zoeal survivorship appears to be increasingly influenced by zoeal density after the molt to stage IV (Figure 114). As zoeae develop they become progressively larger (Table 61) and result in greater biomass in each culture. Stage IV zoeae may represent a critical biomass beyond which zoeal survival is adversely affected. Using standard culture conditions (Table 55), the molt to stage IV occurs on about day 24 (Figure 115). To reduce biomass and improve survival, perhaps slow-developing zoeae should be culled from cultures at this time.

Ovigerous crabs were captured from five locations along the Pacific coast (Table 56). There was no positive correlation between survivorship of zoeae in small-scale mass cultures and origins of the female parent crabs. This concurs with a previous study (Ebert et al. 1975) which shows that larval hatching success and female parent origin were not significantly related.

Spine breakage was a problem in both the sand- and screen-substrate cultures and probably contributed significantly to zoeal mortality. Hartman (1977) also observed zoeae with broken spines and reported a positive relationship between spine breakage and mortality. He suggested that removing overhead lighting might eliminate the problem. However, the problem appears to be related more to sudden lighting changes or to culture perturbations from routine sampling and feeding regimens. The former may be controllable (e.g., continuous lighting or darkness), but the latter would be difficult to circumvent.

The "stunting" of laboratory-reared zoeae remains a problem. Size differences were most evident with laboratory-hatched 1977 zoeae and less evident with laboratory-hatched 1979 zoeae. Stunting may be related to culturing zoeae in a confined area, inadequate diet, or physiological conditions of the cultured zoeae.

Size differences between 1977 and 1979 laboratory-reared zoeae may be a function of food quality or zoeal physiology and genetics. All zoeae in both groups (1977 and 1979) were fed a single-item diet of brine shrimp nauplii from San Francisco Bay brand cysts; however, the cysts were from different batch lots. Possibly, certain batch lots have better quality cysts (and nauplii) than others (Johns et al. 1980). Also, these two groups of laboratory-reared zoeae had different origins. Parent origin data for the 1977 zoeae were not recorded, but these zoeae probably were from several zoeal cultures. The 1979 zoeae were from a San Francisco area female that spawned her eggs in the laboratory. These differences in origin and egg-holding conditions could result in significant physiological and genetic differences as well as concomitant size differences of zoeae.

Our laboratory-cultured zoeae were also smaller than those of previous investigators. Poole (1966) reported stage V zoeae to have a total length of 9.0 mm, and Hartman (1977) reported a mean total length of 9.57 mm. Our stage V zoeae were 6.89 mm (1977) and 8.49 mm (1979).

MEGALOPAL STUDIES

Methods and Materials

Collecting and Handling

Both field-caught and laboratory-reared megalopae were used for studies we conducted from 1974 to 1980.

Field-caught megalopae are generally available during the late-spring to early-summer period off central and northern California. The later stages commonly

swarm in surface waters (Hatfield, Chapter 7), are thigmotactic, and frequently are found in association with drifting kelp or other flotsam. Substantial numbers of megalopae were collected in association with drifting kelp in June 1974 off central California (Russian River area). These were dipnetted by a commercial fisherman, transported to Bodega Bay, and maintained overnight in plastic buckets with aeration. The following day they were transported to the MCL in styrofoam ice chests. During the 5-hr transit period they were immersed in seawater, but had no aeration or chiller bags.

Laboratory-reared megalopae were used from 1975 to 1980. These were removed from zoeal-culture systems within 24 hr of achieving this stage because they prey on zoeae. Megalopal removal was accomplished with a wide-bore (8-mm id) pipette.

Culture Systems

Four methods for culturing megalopae were tested: (i) 250-ml flasks, (ii) 1.3-m² troughs, (iii) PVC pipe sections held in a care-o-cell, and (iv) a compartmented plastic tray. Extensive testing was performed with the latter two methods, which are described in detail. Megalopal cultures in these two systems received a continuous flow of 20- μ m-filtered, UV-treated seawater from an overhead source. The standard temperature was 14 ± 1 C, although some cultures were maintained at 15 C and 16 C. Water depth was relatively shallow, being only 2 to 4 cm.

Pipe Sections. PVC pipe sections (cells) were either 5- or 8-cm diameter (Table 62). The cells were held in a rotating care-o-cell system adapted from Van Olst et al. (1976). The care-o-cell consists of a floating carriage, buoyed by styrofoam blocks, which rotates about a central axis and is propelled by overhead water jets. The carriage was 1.2-m diameter and held either 75 8-cm or 165 5-cm diameter cells.

Substrate, density, and diet experiments were conducted in the cells. Two substrates were tested: (i) Nitex screening (405 μ m); and (ii) perforated plastic sheeting (Penn-Plax aquarium dividers; perforations 1.0 mm diameter and 3.0 mm apart). Four megalopal densities were tested, 1, 2, 3, and 6 megalopae per cell. The standard diet was adult brine shrimp (about 20 per cell). Five other food items were tested in various combinations (Tables 62 and 63). Diets were evaluated according to megalopal survivorship. Cells were cleaned three or four times per week just prior to each feeding.

Sizes of these laboratory-reared megalopae were measured in 1977 and 1979. These were compared with 1977 field-caught megalopae.

Plastic Tray. A styrene plastic tray was partitioned into four equal compartments (Table 62). The tray had a fiberglass window-screen bottom that was elevated and supported to facilitate water passage. The screen was covered with sand (2.5 cm deep) which served as a substrate for the megalopae. Water entered each compartment in a continuous flow (250 ml/min) on the surface and exited through the sand substrate.

Culture success was evaluated at two megalopal densities (9 and 18 per compartment), and with three food items (adult brine shrimp, brine shrimp nauplii, and benthic diatoms) presented in various combinations.

TABLE 62. Culture Parameters Tested with Megalopae in PVC Pipe Sections and a Compartmented Plastic Tray.

Culture parameter	Pipe sections	Compartmented plastic tray
Substrate	Nitex screen	Sand (2.5 cm deep) over fiberglass window screen.
Dimensions	Perforated plastic sheet 5 cm (id) $\times$ 5.5 cm high 8 cm (id) $\times$ 7.5 cm high	35 $\times$ 26 $\times$ 13 cm deep/compartment
Substrate area	20 cm ² 50 cm ²	910 cm ² /compartment
Temperature	14 $\pm$ 1 C 15 $\pm$ 1 C	14 $\pm$ 1 C 16 $\pm$ 1 C
Megalopal density	0.05/cm ² 0.10/cm ² 0.15/cm ² 0.30/cm ²	0.01/cm ² 0.02/cm ²
Diet	Live adult brine shrimp (20/cell) * Dried brine shrimp (2 cm ² /cell) † Dried blue-green algae (2 cm ² /cell) § Squid (3 cm ³ /cell) ¶ Cladocera (20/cell) # Tofu (3 cm ³ /cell) **	Live adult brine shrimp (700/compartment) Brine shrimp nauplii (20/ml) † Benthic diatoms (2-cm ² sheets/compartment)

* From San Francisco Bay.

† Freeze dried adults, San Francisco Bay brand.

‡ Laboratory-hatched from San Francisco Bay brand cysts.

§ *Spinulina platensis* supplied by Proteus Corp., Berkeley, CA.

¶ Mostly naviculoids.

¶ Frozen (thawed) *L. opalescens*.

Unknown freshwater species.

** Soybean curd.

TABLE 63. Megalopal Survivorship to First Crab Instar in Substrate, Density, and Diet Experiments in the Care-o-cell Culture System.

Experiment and substrate	No. of cells	Cell substrate area (cm ²)	Megalopal density		Diet	Mean survival (%)
			No./cell	No./cm ²		
Substrate						
405 μ m-Nitex	38	50	1	0.02	Brine shrimp adults	58
Perforated plastic sheet	27	50	1	0.02	Brine shrimp adults	52
Density						
405 μ m-Nitex	50	20	1	0.05	Brine shrimp adults	92
405 μ m-Nitex	108	20	2	0.10	Brine shrimp adults	82
405 μ m-Nitex	5	20	3	0.15	Brine shrimp adults	53
405 μ m-Nitex	5	20	6	0.30	Brine shrimp adults	30
Diet						
405 μ m-Nitex	3	50	1	0.02	Squid	0
405 μ m-Nitex	3	50	1	0.02	Tofu	0
405 μ m-Nitex	3	50	1	0.02	Cladocera	0
405 μ m-Nitex	5	50	2	0.10	Brine shrimp adults and dried blue-green algae	40
405 μ m-Nitex	5	20	2	0.10	Dried brine shrimp	10
405 μ m-Nitex	5	20	2	0.10	Dried blue-green algae	0
405 μ m-Nitex	5	20	2	0.10	Dried brine shrimp and dried blue-green algae	0

Results

Collecting and Handling

Nearly all field-caught megalopae survived transit to the laboratory. However, most metamorphosed to the first crab instar while in transit and the remainder within the following 24 hr. These were used for crab instar studies.

Laboratory-raised stage V zoeae tended to metamorphose to the megalopal stage at night. These megalopae were removed each morning. It was not uncommon to find zoeae in the grasp of megalopae and, presumably, some zoeal mortality occurred before all megalopae were removed.

Culture Systems

Megalopae cultured in 250-ml flasks and 1.3-m² troughs suffered high mortalities due to fouling with bacteria and fungus. After preliminary experimentation, these culture methods were abandoned and our efforts focused on PVC pipe sections and plastic tray cultures.

Pipe Sections. Substrate experiments revealed nearly equal megalopal survival on Nitex screening and perforated plastic sheeting (58% and 52%, respectively) to the first crab instar (Table 63).

Density experiments showed an inverse relationship between megalopal concentration and survival (Table 63). Megalopal densities greater than 0.10/cm² resulted in poor culture success. Very few megalopal mortalities were directly attributable to cannibalism (e.g. megalopae observed with missing or broken appendages).

Adult brine shrimp proved to be a satisfactory diet for megalopae. The other five food items were unsatisfactory (Table 63).

Megalopal development rate was directly related to temperature. Megalopae cultured at 14 ± 1 C averaged 22.9 days (range 14 to 33 days) to molt to the first crab instar while megalopae cultured at 15 ± 1 C averaged only 18.8 days (range 13 to 29 days) in this stage.

Laboratory-reared 1977 and 1979 megalopae were smaller than 1977 field-caught megalopae. In fact, the 1977 laboratory-reared megalopae were smaller than both the 1979 laboratory-reared and the 1977 field-caught megalopae (Table 64).

The fungus *Lagenidium* sp. did not appear to infect megalopae in these pipe-section cultures.

Plastic Tray. Density experiments showed an inverse relationship between megalopal density and survival (Table 65).

Of the four diets examined (Table 65), the best megalopal culture success (89% survival) occurred with adult brine shrimp. Poorest survival (22%) occurred with a diet of brine shrimp nauplii and benthic naviculoid diatoms. Although the diatoms multiplied and eventually coated the sand substrate, we were unable to detect whether megalopae fed on them. Extraneous organisms such as nematodes and ciliate protozoans also were noted; these possibly were introduced with the diatoms.

TABLE 64. Sizes of Field-caught 1977 Megalopae and Laboratory-reared 1977 and 1979 Megalopae.

<i>Megalopae origin</i>	<i>No. measured</i>	<i>Length (mm) *</i>		<i>Width (mm)†</i>	
		$\bar{x}$	<i>range</i>	$\bar{x}$	<i>range</i>
Field caught					
1977‡	50	6.67	6.01–7.15	4.07	3.31–4.70
Laboratory reared					
1977 ‡	8	4.70	4.33–5.00	2.82	2.65–3.14
1979	10	5.14	4.93–5.52	3.04	2.83–3.25

* Distance from tip of rostral spine to posterior carapace edge (excluding dorsal spine).

† Greatest carapace width.

‡ Measured by Paul N. Reilly, Calif. Dep. of Fish and Game, Menlo Park, CA.

TABLE 65. Megalopal Survivorship to First Crab Instar in Density and Diet Experiments in the Compartmented Plastic Tray Culture System.

<i>Experiment</i>	<i>Megalopal density</i>		<i>Diet</i>	<i>Mean survival (%)</i>
	<i>No./compartment</i>	<i>No./cm²</i>		
Density	9	0.01	Brine shrimp adults, brine shrimp nauplii, and benthic diatoms	50
	18	0.02	Brine shrimp adults, brine shrimp nauplii, and benthic diatoms	26
Diet	9	0.01	Brine shrimp adults	89
	9	0.01	Brine shrimp nauplii	67
	9	0.01	Brine shrimp adults and benthic diatoms	78
	9	0.01	Brine shrimp nauplii and benthic diatoms	22

Five possible cases of cannibalism were detected in the plastic tray cultures; there was no apparent correlation with stocking density. Also, megalopae in these cultures were generally free of the fungus *Lagenidium* sp.; only one megalopa was observed to be infected.

Discussion

Megalopal culture methods were not investigated intensively compared to our zoeal studies. Most megalopae were cultured in plastic pipe sections (cells) with Nitex screen substrates in the care-o-cell culture system. This system proved to be the most satisfactory for maintenance. However, it was often difficult or impossible to compare culture systems (care-o-cell vs. compartmented plastic tray) with culture success (megalopal survival) due to experiment design.

Nitex screening and perforated plastic sheeting were equally acceptable substrates for megalopal culture. Unfortunately, we did not make direct comparisons of these substrates to sand with regard to megalopal survivorship. However, sand substrate cultures were relatively difficult to maintain, particularly from a sanitary viewpoint. The sand tended to harbor "contaminants", e.g. decaying

food particles, ciliates, and nematodes. These may have affected megalopal survivorship. Also, the megalopae blended with or partially buried in the sand, compounding observation problems.

Density experiments using both culture methods revealed an inverse relationship between numbers of megalopae and survivorship. However, megalopal survivorship in the care-o-cell was considerably better at greater megalopal densities than in compartmented plastic tray cultures. We suspect that sand substrate and the resulting problems encountered in maintaining good sanitary conditions were responsible for this poor culture success.

Seawater culture temperature experiments were conducted over a very limited range. Although these experiments revealed that megalopae developed faster at a higher temperature, we did not determine an optimum culture temperature.

Diet experiments with both culture systems showed that adult brine shrimp comprised an adequate diet for megalopae. Other diets or diet combinations generally were unacceptable. The stunting of laboratory-cultured megalopae, compared to field-caught megalopae, is possibly diet-related. Similar stunting was obvious in crab zoeae. Megalopal stunting likely represents a progression of the stunting observed in zoeae.

Although our megalopal culture studies were limited, they were of sufficient scope to present some criteria for successful experimental culture. Included are: (i) a care-o-cell culture system; (ii) low-profile plastic pipe section culture containers (larger-diameter cells, up to 20 or 30 cm in diameter, also can be used conveniently); (iii) Nitex screen substrate (about 0.5-mm mesh); (iv) a stocking density of 0.10 megalopae/cm²; (v) an adult brine shrimp diet; and (vi) seawater temperature of 14 to 15 C.

POSTLARVAL INSTAR STUDIES

Methods and Materials

Culture Systems

Postlarval instar culture systems were identical, or similar, to those used for megalopae, particularly for the early instars (Table 66; nos. 1, 3, 4, 6, 7 and 8). However, later instars were cultured in systems having a greater capacity (Table 66; no. 2). All experiments were done using thru-flow systems with seawater either at ambient temperature (10 to 15 C) or constant temperature (14 C $\pm$ 1 C) from an overhead source. Filtered (20 μ m) and unfiltered (raw) seawater were used. Seawater flow rates were not closely regulated, but were considered to exceed minimal requirements. Sand substrate cultures (Table 66; nos. 2 and 5) incorporated a subsand, airlift filtration system. Culture systems and experiments were designed primarily to measure or compare (i) instar growth and survival, (ii) cannibalism, (iii) habitats (as a method to reduce cannibalism), (iv) substrate types, and (v) dietary preferences. In this section, the word "instar" is used to denote postlarval crab stages.

Growth and Survival

Three instar year classes (1974, 1975, and 1976) were used for growth rate information. The 1974 year-class instars were field-caught as megalopae and

TABLE 66. Postlarval Instar Culture Systems Tested From 1974 to 1980.

System no.	System description	Container dimensions (cm)			Bottom surface area (cm ²)	No. of compartments	Culture temperature (C)	Seawater treatment
		length	width	depth				
1	Compartmented plastic box; fiberglass screen substrate	13	8	10	104	32	Ambient (10-15) or constant (14 ± 1)	Filtered (20 μm)
2	Compartmented wooden trough, plastic laminated; sand substrate	27	19	20	513	44	Ambient (10-15)	Unfiltered
3	Care-o-cell;* Nitex screen or perforated plastic sheet substrate	-	8	8	50	75	14 ± 1	Filtered (20 μm)
4	Compartmented plastic box; sand substrate	20	14	13	280	4	14 ± 1	Filtered (20 μm)
5	PVC pipe section; Nitex screen substrate with AstroTurf overlay	-	20	13	324	1	14 ± 1	Filtered to instar VI; unfiltered thereafter.
6	Fiberglass aquarium; 75 liter capacity; sand substrate	48	41	26	1,968	1	Ambient (10-15)	Filtered (20 μm)
7	PVC pipe section; Nitex screen (140 μm) substrate with or without sand overlay	-	8	8	50	18	14 ± 1	Filtered (20 μm)
8	Compartmented fiberglass trays; fiberglass screen substrate	8	8	5	64	40	Ambient (10-15) and constant (14 ± 1)	Filtered (20 μm) and unfiltered.

* Described in text under "megalopal culture systems."

reared through instar IV in system no. 1 (Table 66), one per compartment, and fed adult brine shrimp. At instar V they were transferred to a tank with larger compartments and sand substrate (Table 66; system no. 2), one crab per compartment, and were fed a diced squid diet.

The 1975 year-class instars were laboratory hatched and reared to instar VII, one per compartment, in the same compartments as the 1974 year class. The adult brine shrimp diet was supplemented with squid at instars II and III, but these crabs were fed only squid thereafter. At instar VIII they were transferred to larger compartments (Table 66; no. 2).

The 1976 year class was also laboratory hatched, but these instars were reared in the "care-o-cell" system (Table 66; no. 3), one per compartment and were fed the same diet as the 1975 year class. They were transferred to larger compartments (Table 66; no. 2) at instar VII.

For all three year classes, crabs were examined daily. Upon molting, exuviae were removed and measured for carapace width. The measurement was made just anterior to the 10th anterolateral spines and recorded to the nearest 0.1 mm.

Cannibalism

Three culture systems were used to measure instar cannibalism (Table 66; nos. 4, 5, and 6). Diet rations were adjusted so that an excess always remained. Experiments were monitored daily for cannibalism and to remove and measure exuviae.

Experiment #1: Cannibalistic behavior and methods to reduce cannibalism were examined by using different habitats. The culture container had sand substrate and was divided into four equal compartments. Giant kelp, *Macrocystis* sp., blades were added to one compartment; another compartment had littleneck clam, *Tapes* sp., valves; a third compartment had plastic pipe fittings and plastic grating (12-mm grid); while the remaining compartment served as the control. Four instar I crabs were placed in each compartment at a density of 1/70 cm². Diced market squid, *Loligo opalescens*, and giant Pacific oyster, *Crassostrea gigas*, were supplied daily.

Experiment #2: AstroTurf substrate was tested as a method to reduce cannibalism. Fifteen instar I crabs were put in this culture (1/21 cm²). Adult brine shrimp served as their diet to about instar VI or VII, diced squid thereafter.

Experiment #3: A 75-liter aquarium was used as the culture container. Thirty instar I crabs were put in the aquarium (1/67 cm²). A diced squid diet was provided daily.

Substrate Experiments

Two substrate types, sand and 140- μ m Nitex screen, were used to compare survivorship, growth, and equilibrium (a few crabs had tended to repose upside down). Experiments commenced with the megalopal stage to insure an instar source that had not been exposed to sand during larval development.

Two groups of megalopae were raised communally in 20-cm diameter PVC pipe sections. One group of 20 was cultured on Nitex screen; a second group comprised of eight megalopae was raised on sand substrate. Upon attaining instar I, both groups were transferred to individual compartments (Table 66; no.

7). One-half of the instars raised on Nitex were retained on this substrate, the other half were transferred to sand substrate. Similarly, one-half of the instars that had been raised on sand remained on this substrate, the other half were transferred to Nitex.

Crabs in these systems were fed adult brine shrimp and diced squid.

Diet Studies

Diet experiments were conducted in 1974, 1975, and 1976 to compare early instar survival and growth.

The 1974 year-class instars were field-caught as megalopae and the experiments were conducted in compartmented trays, one crab per compartment. These crabs were divided into three groups: one group of 32 (Table 66; no. 1); and two groups of 20 (Table 66; no. 8). Seawater type was also compared (20 μm filtered to unfiltered) to diet with the latter two groups. The filtered seawater was maintained at 14 ± 1 C; the unfiltered at ambient temperature (11–14 C). The group of 32 crabs (Table 66; no. 1) were fed adult brine shrimp (live from San Francisco Bay). The other two instar groups received either squid (frozen) or oyster (fresh), or a combination of these. Brine shrimp were presented daily (about 15 to 20 per crab), and the squid and oyster diced (1 cm^2) and offered on alternate days, one piece per crab. Uneaten brine shrimp fragments were removed daily; uneaten squid and oyster were removed just prior to the next feeding.

The 1975 and 1976 year-class instars were laboratory hatched and reared. They were held in individual compartments similar to those used in 1974. They were supplied with filtered seawater (20 μm) and the culture temperature was maintained at 14 ± 1 C. These crabs were fed adult brine shrimp at instar I, a combination of brine shrimp and squid at instar II and III; and squid thereafter. Food quantities and sanitary procedures followed those of 1974.

Results

Growth and Survival

The 1974 year-class crabs, field caught as megalopae and laboratory reared, were significantly larger than both the 1975 and 1976 laboratory-hatched-and-reared year classes at comparable instars (Figure 117; Tables 67, 68, and 69). Poorest growth was exhibited by the 1976 year class. This year class also metamorphosed from megalopa to instar I at a smaller size than the other two year classes.

The intermolt periods of 1974 year-class crabs were slightly longer than either the 1975 or 1976 year classes. An average 1974 year-class instar was almost 1-year old (excluding the larval period) at instar IX. However, similarly-aged 1975 and 1976 year-class crabs were in instars X and XII, respectively. Intermolt periods for all crabs progressively increased at successive instars (Tables 67, 68, and 69). Protracted intermolt periods for individual crabs generally signaled impending mortality.

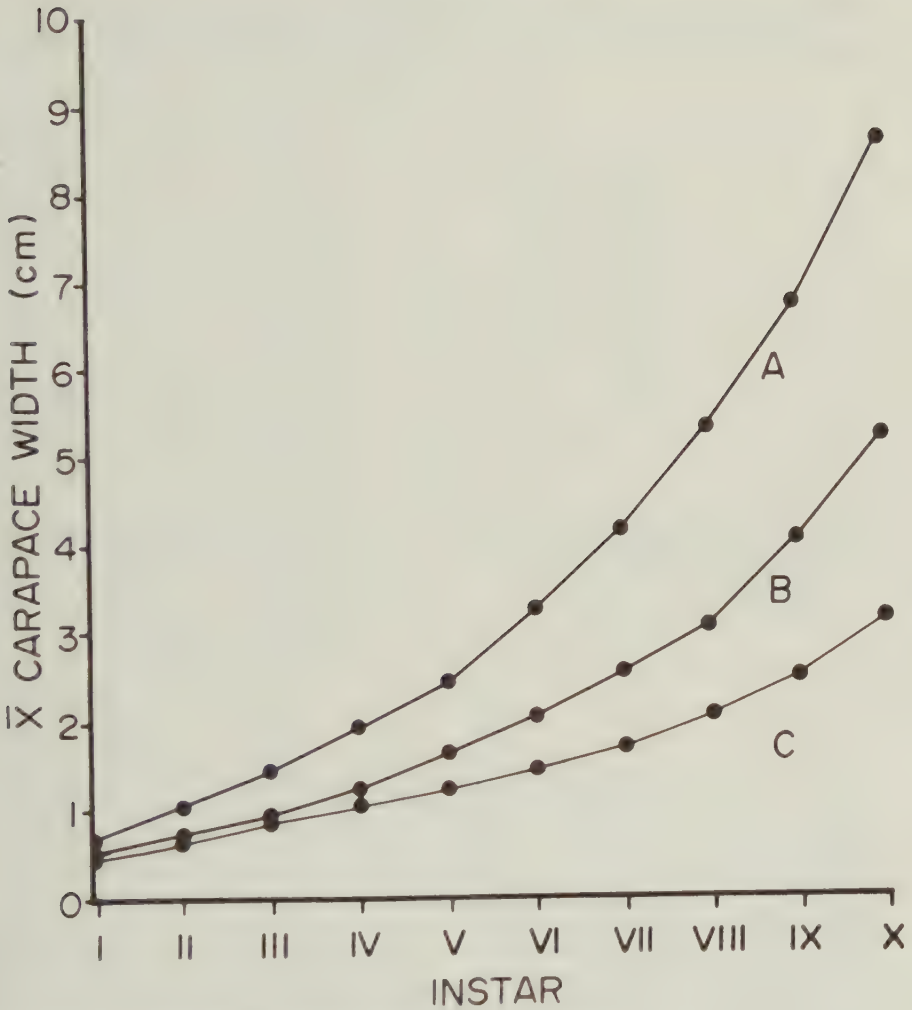


FIGURE 117. Growth rates of laboratory-cultivated Dungeness crabs. A=1974 year class; B=1975 year class; C=1976 year class.

Survival generally was good through the first six or seven instars, but poor beyond instar X or XI. At times, seawater inlets clogged and reduced water flows or drains clogged and caused flooding, indirectly causing substantial mortality. Also, crab exoskeletons frequently developed dark-brownish colored lesions or eroded areas (commonly called "black rot"), particularly on the dactyls and in later instars. Very few crabs survived to instar XV.

One female crab from the 1974 year class was maintained for nearly 3.5 years and died in instar XIII. During this time this crab mated twice and spawned three times. Each spawning resulted in a viable larval hatch (Table 70).

TABLE 67. Laboratory Growth Rates of Dungeness Crab Instars Field-caught as Megalopae in 1974.

Instar	No.	%	Carapace width (mm) *		Intermolt period (days)	
			$\bar{x}$	Range	$\bar{x}$	Range
I	32	100	6.9	6.0- 7.5	17	13- 20
II	32	100	10.5	9.1- 11.8	16	14- 18
III	32	100	14.3	12.2- 15.9	16	14- 18
IV	32	100	19.2	15.9- 22.0	20	13- 26
V	31	97	24.7	20.8- 28.9	28	21- 43
VI	28	88	32.8	26.8- 39.4	33	27- 74
VII	27	84	42.0	35.2- 53.2	78	36-149
VIII	18	56	53.6	45.9- 68.5	82	51-143
IX	15	47	67.7	59.5- 79.2	71	46-121
X	15	47	86.2	75.7-100.5	82	55-108
XI	12	38	107.4	96.4-130.7	174	94-294
XII	6	19	124.2	112.3-132.2	-	-
XIII	2	6	142.2	136.2-148.3	-	-

* Excludes spines.

TABLE 68. Growth Rate of Dungeness Crab Instars from a 1975 Laboratory Hatch.

Instar	No.	%	Carapace width (mm) *		Intermolt period (days)	
			$\bar{x}$	Range	$\bar{x}$	Range
I	28	100	5.2	4.6- 6.0	14	11- 19
II	28	100	7.3	6.3- 8.2	12	8- 20
III	27	96	9.7	8.7-11.0	13	10- 31
IV	26	93	12.7	11.2-14.7	17	12- 33
V	23	92	16.4	14.3-19.6	20	10- 36
VI	21	84	20.6	16.7-25.2	28	19- 50
VII	18	72	25.6	19.8-31.9	49	32- 93
VIII	8	32	30.9	22.8-40.3	56	37-108
IX	7	28	40.6	31.0-50.1	60	37- 84
X	6	24	52.4	40.2-66.1	73	35- 96

*Excludes spines.

TABLE 69. Growth Rate of Dungeness Crab Instars from a 1976 Laboratory Hatch.

Instar	No.	%	Carapace width (mm) *		Intermolt period (days)	
			$\bar{x}$	Range	$\bar{x}$	Range
I	31	100	4.9	4.1- 5.4	15	11-21
II	30	97	6.6	5.4- 7.2	15	12-17
III	30	97	8.4	7.1- 9.2	15	13-21
IV	22	71	10.3	8.8-11.2	21	14-48
V	21	68	12.4	10.5-13.4	22	15-35
VI	20	64	14.8	12.8-16.2	21	16-29
VII	20	64	17.4	14.0-19.2	24	19-32
VIII	20	64	21.0	16.0-23.7	33	23-47
IX	19	61	25.8	18.9-29.8	42	32-65
X	18	58	32.4	24.8-37.5	60	42-85
XI	14	45	40.4	31.0-47.6	62	50-79
XII	13	42	52.3	37.7-64.8	55	50-66
XIII	8	26	63.0	46.4-69.7	-	-

*Excludes spines.

TABLE 70. Growth and Life History Information for a Female Dungeness Crab Field-captured as a Megalopa in 1974 and Laboratory-cultivated for 3.5 Years.

Date	Instar	Instar duration (days)	Carapace width (mm) *	Reproductive state
06/18/74	I	15	7.2	Immature
07/04/74	II	16	11.3	Immature
07/20/74	III	17	15.5	Immature
08/06/74	IV	25	21.1	Immature
09/01/74	V	34	26.4	Immature
10/04/74	VI	29	36.1	Immature
11/02/74	VII	62	47.1	Immature
01/04/75	VIII	70	59.9	Immature
03/15/75	IX	84	79.2	Immature
06/07/75	X	93	99.8	Immature
09/08/75	XI	293	119.1	Mature—first mating
12/23/75	XI	—	119.1	Spawned
04/03/76	XI	—	119.1	Larval hatch commenced
06/25/76	XI	—	119.1	Premating
06/29/76	XII	455	132.2	Second mating
10/25/76	XII	—	132.2	Spawned
12/30/76	XII	—	132.2	Larval hatch commenced
04/29/77	XII	—	132.2	Spawned (without mating)
06/30/77	XII	—	132.2	Larval hatch commenced
09/27/77	XIII	—	148.3	Unsuccessful mating attempt
12/01/77	XIII	—	148.3	Crab died

* Excludes spines.

Cannibalism

Experiment #1: All crabs completed the first two molts to instar III. At this stage cannibalism became evident. The experiment had been in progress for 30 days. Seven crabs were cannibalized at stage III: three in the compartment with clam valves; two in the control compartment; and one in each of the remaining two compartments. One crab died from unknown causes in the kelp blade compartment. Cannibalism typically occurred during the molting period when crabs were in a soft-shell condition. Excess food was present in each compartment at the time of cannibalism. The crabs exhibited a preference for squid over oyster and most of the squid usually was consumed. Aggression between instar III crabs also was evident and occasionally resulted in appendage losses that impaired locomotion and made these crabs more vulnerable to cannibalism. After 52 days, seven (50%) had been cannibalized (Table 71). Seven of the eight remaining crabs molted to instar IV when the experiment was disrupted by flooding and terminated.

Experiment #2: Cannibalism was first noted after the experiment had been in progress for 50 days and crabs were instars II and III. Cannibalism continued at a constant rate over the remainder of the experiment (157 days). When the experiment was terminated, 11 crabs had been cannibalized (Table 71), two died from unknown causes, and two instar IX crabs remained (both females).

Table 71. Cumulative Cannibalism Rates.

Elapsed time (days)	Experiment #1		Experiment #2		Experiment #3	
	no.	%	no.	%	no.	%
20	0	0	0	0	5	17
40	5	36	0	0	6	20
60	7	50	1	8	12	40
80	—	—	3	25	17	57
100	—	—	5	42	21	70
120	—	—	6	50	24	80
140	—	—	9	75	26	87
160	—	—	11	92	—	—

Experiment #3: The first crab mortality was observed 4 days after the experiment began. The dead crab had several appendages missing, probably the result of an aggressive interaction rather than cannibalism. Cannibalism was not actually observed in the ensuing months of the experiment, but was evident from near-daily counts that showed fewer crabs. After the experiment had been in progress for 40 days, 23 (77%) of the original 30 remained. After 90 days, only 10 crabs (30%) remained. Smaller crabs frequently were noted with missing appendages. Instar V (and possibly VI) crabs were present at this time, although exact instar composition was not determined. During the 3rd and 4th months of the experiment (90 to 112 days), the crab population was reduced to six (20% survival), and cannibalism of a recently molted (soft-shell) crab was observed for the first time. Carapace widths of exuviae during this period ranged from 19.0 to 29.5 mm ($\bar{x} = 25.0$ mm), suggesting that most crabs were at instar VI. The experiment continued about three more weeks (total of 140 days) and was terminated with four crabs (about 13%) remaining (Table 71). Exuviae from these crabs had a mean carapace width of 34 mm, suggesting instar VII.

Substrate Experiments

Crabs raised on sand substrate grew faster than those raised on Nitex, although survival was better on Nitex than sand. Mean carapace widths of instar V crabs were very similar for all crabs irrespective of substrate type (Table 72). Crab equilibrium problems were not evident on either sand or Nitex substrates, regardless of the megalopal substrate type.

TABLE 72. Survival, Growth, and Developmental Rate as a Function of Substrate.

Substrate		No. of crabs		$\bar{x}$ Instar carapace width (mm) *					$\bar{x}$ Days to instar V
Megalopae	Crab instars	Start	End	I	II	III	IV	V	
Nitex	Nitex	5	5	6.1	8.9	11.5	14.6	18.3	106
Nitex	Sand	5	2	6.1	9.2	11.7	15.2	19.8	93
Sand	Sand	4	2	5.6	8.4	10.5	14.0	18.7	94
Sand	Nitex	4	4	5.6	8.1	10.5	13.2	17.1	104

* Excludes spines.

A "gas bubble disease" (Fickeisen et al. 1980) problem occurred in all substrate cultures at the megalopal stage due to a faulty pump-suction hose. This problem was corrected by baffling the seawater supply to dissipate excess gasses.

Diet Studies

The 1974 diet experiments revealed that crabs fed only adult brine shrimp had the best survival (97%) at instar V, averaged larger carapace width (24.9 mm) at instar V, and had the shortest intermolt periods (Table 73). Growth and survival with the squid and oyster diets, singly or combined, were less satisfactory. Diets containing oyster resulted in 20% and 0% survival at instar V for those receiving raw and filtered seawater, respectively (Tables 73 and 74). These experiments overall revealed that crabs cultured in raw seawater survived better and grew faster than those cultured in filtered seawater (Tables 73 and 74).

The 1975 and 1976 laboratory-hatched instar I crabs were stunted compared to the 1974 field-caught crabs. Therefore, diets were not compared between crabs from these two different origins. The standard diet regimen presented to 1975 and 1976 year-class instars likely was satisfactory. However, in 1975, survival to instar V was 92%; in 1976, it was only 68%.

TABLE 73. Growth and Survival of Instars I-V Fed Different Diets and Receiving Filtered Seawater.

Diet	Instar	Survival		Carapace width (mm) *		Intermolt period (days)	
		No.	%	$\bar{x}$	Range	$\bar{x}$	Range
Adult brine shrimp †	I	32	100	6.9	6.0- 7.5	17	13-20
	II	32	100	10.5	9.1-11.8	16	14-18
	III	32	100	14.3	12.2-15.9	16	14-18
	IV	32	100	19.2	15.9-22.0	20	13-26
	V	31	97	24.9	20.8-28.9	28	21-43
Squid ‡	I	10	100	6.9	6.4- 7.5	19	15-22
	II	10	100	9.8	9.0-10.6	26	21-27
	III	9	90	14.5	11.8-14.2	25	18-24
	IV	9	90	16.9	14.9-18.1	27	22-37
	V	4	40	21.7	19.0-23.2	-	-
Oyster §	I	5	100	6.8	6.5- 7.1	17	15-18
	II	4	80	9.6	9.2- 9.9	64	52-71
	III	3	60	12.1	11.2-13.2	-	-
	IV	0	0	-	-	-	-
	V	0	0	-	-	-	-
Squid plus oyster	I	5	100	7.0	6.2- 7.7	17	14-23
	II	5	100	10.1	9.0-11.5	38	27-62
	III	5	100	12.2	10.6-14.2	39	34-44
	IV	3	60	17.0	14.7-19.1	-	-
	V	0	0	-	-	-	-

* Excludes spines.

† Live from San Francisco Bay.

‡ *Loligo opalescens* (frozen), about 1-cm³ piece per crab per day.

§ *Crassostrea gigas* (fresh), about 1-cm³ piece per crab per day.

TABLE 74. Growth and Survival of Instars I-V Fed Different Diets and Receiving Unfiltered Seawater.

Diet	Instar	Survival		Carapace width (mm) *		Intermolt period (days)	
		No.	%	$\bar{x}$	Range	$\bar{x}$	Range
Squid †	I	9	100	6.9	6.3- 7.3	18	14-24
	II	9	100	9.9	9.2-10.7	24	21-31
	III	9	100	13.3	12.5-14.4	25	19-43
	IV	9	100	17.3	16.3-18.9	28	22-30
	V	9	67	22.9	21.5-23.7	-	-
Oysters ‡	I	5	100	6.8	6.6- 7.0	16	14-18
	II	5	100	10.1	9.7-10.6	28	21-35
	III	5	100	12.8	11.9-13.6	37	30-44
	IV	4	80	17.1	16.0-18.2	28	28-28
	V	1	20	23.5	23.5-23.5	-	-
Squid plus oyster	I	5	100	6.7	6.4- 7.2	17	15-20
	II	5	100	9.8	9.3-10.3	29	20-46
	III	5	100	12.7	11.1-14.0	32	32-41
	IV	3	60	16.0	14.8-16.8	28	28-28
	V	1	20	21.1	21.1-21.1	-	-

* Excludes spines.

† *Loligo opalescens* (frozen), about 1-cm² piece per crab per day.‡ *Crassostrea gigas* (fresh), about 1-cm² piece per crab per day.

Discussion

Growth and Survival

Stunting of laboratory-hatched-and-reared crabs, when compared to field-caught crabs, was evident in initial larval stages and persisted through the crab instars. The severest stunting was observed in the 1976 year class and became even more pronounced at instar IV when compared to the 1975 year class. Both instar groups were cultured identically. It is difficult to surmise why instar stunting was greater in 1976, but it could be related to larval culture differences. We generally did not maintain life history records tracing crab offspring from the hatch through the larval and postlarval stages. Another aspect of stunting that was obvious, but not understood, was the direct relationship between intermolt period and stunting. The shortest intermolt periods (through instar X) occurred with the 1976 year class. Correspondingly, the smallest incremental increases in carapace width between molts occurred with these same crabs.

Stunting of the laboratory-cultured 1974 year-class crabs, which were field-caught as megalopae, was also evident, but not as pronounced. Poole (1967) reported that wild population instars from the Bodega Bay area had mean carapace widths of 15.8 mm, 28.3 mm, and 63.4 mm at instars III, V and VIII, respectively. Our 1974 year-class crabs at instars III, V, and VIII had respective carapace widths of 14.3 mm, 24.7 mm, and 53.6 mm. Furthermore, Poole reported that the male instar XIII (mature males grow faster than females; Collier, Chapter 9) from the commercial fishery had a mean carapace width of 169.9 mm. Our stage XIII males (1974 year class) had a mean carapace width of 142.4 mm. This size is roughly 10 mm less than Poole reported for male instar XII. Poole did indicate crab instar growth rates may differ considerably from year to year and that year-class strength tended to be related to growth rate variation.

Aside from mechanical problems with cultures that contributed to crab mortality in the later instars, the extended intermolt period of these stages probably was an indirect mortality factor. These older crab exoskeletons were often fouled and eroded and gave the crabs an unhealthy appearance. These crabs often appeared sluggish and their mobility was frequently impaired by "black rot". A chitinoclastic bacteria is believed responsible and may have indirectly contributed to mortality.

Poole (1967) believed instar XV to be the final stage in a crab's life, but calculated instar XVI as the final stage based on width-frequency distributions. We cultivated a number of crabs to instar XV, a few to XVI, and one to XVII. However, all were severely stunted compared to the wild population.

Cannibalism

Cannibalism was difficult to measure in the aquarium (cannibalism experiment no. 3) due to the greater number of crabs, large surface area, and because crabs buried in the sand substrate. The only clue to cannibalism was the declining number of crabs that were counted. Cannibalism was easier to measure in the other two experiments. The onset of cannibalistic tendencies was readily observed and was signaled by increased aggressive behavior among crabs. The experimental habitats did not alleviate cannibalism. It might be presumed that cannibalism is a function of available space or territoriality, but our data do not support this. The crabs often tended to be very aggressive towards one another even when only a few remained, and actively sought out those which were in the post-molt, soft-shell stage. Our data suggest that, after instar II, crabs must be cultured in individual cells to obtain reasonable survival rates. This is labor-intensive for mariculture purposes.

Substrate Experiments

Sand and Nitex screen both were good substrates for crabs although some mortality occurred on sand. It apparently is better to culture the first few instars on Nitex, where sanitary conditions are more easily maintained, then transfer them to sand. We used this procedure for other instar studies and it worked quite well.

Occasionally, laboratory-cultured crabs experienced an equilibrium problem and reposed upside down on the substrate. We had presumed that this behavior was related to substrate and that a sand substrate is required at least by instar V. However, no crabs in this experiment exhibited this behavior. Apparently the equilibrium defect is related to some other, as yet unknown, factor.

The "gas bubble disease" problem noted at the megalopal stage also was observed in other shellfish species in our laboratory. It is widely-reported in the literature (Fickeisen et al. 1980). In the case of crab megalopae, tiny air bubbles form on the gill lamelle and collect under the carapace causing the megalopae to float. The technique of baffling the seawater supply to dissipate excess gasses is commonly used in other hatcheries and laboratories and is effective for megalopae.

Diet Studies

Postlarval instars I through V, fed on a diet of only live adult brine shrimp, showed more favorable growth and survival than crabs presented either squid or oyster diets. The poor growth and survival of crabs presented fresh oysters

suggests that oysters either contain or release an incompatible substance. We do not know whether crab mortality resulted from oyster ingestion or contamination of the water, although the former is more likely because thru-flow culture systems were used.

The 1974 experiments indicate that raw seawater is more favorable than filtered seawater for growth and survival of early postlarval instars. Our experiments suggest that, with crabs fed only squid, water type rather than the squid diet was more likely responsible for crab mortalities after instar IV (Tables 73 and 74). Unfortunately, we did not conduct follow-up experiments to confirm this possibility.

The effect of the feeding regimen for 1975 and 1976 year-class crabs is difficult to analyze. These crabs were cultured from larvae that were laboratory-hatched, whereas the 1974 year class was from field-caught megalopae. These differences in origin undoubtedly influenced growth and survival. The high survival (92%) of 1975 stage V instars (Table 68) indicates that a feeding regimen of only brine shrimp (instar I), then brine shrimp plus squid (instars II and III), and thereafter squid by itself, was satisfactory. Furthermore, the fact that later cultures were conducted in filtered seawater rather than raw seawater did not appear to affect culture success adversely.

From the standpoint of food availability and culture maintenance, the feeding regimen of 1975 and 1976 year-class crabs was more desirable than a strict brine shrimp diet (1974 year class). Adequate quantities of clean, live adult brine shrimp were often difficult to obtain, while frozen squid usually was available. Furthermore, the crabs constantly shredded adult brine shrimp, leaving a residue of broken pieces that had to be removed daily to prevent fouling. This problem was not as evident with squid.

BRINE SHRIMP STUDIES

Methods and Materials

Cyst Origin

From 1971 through 1977, crab larvae were fed brine shrimp nauplii hatched from San Francisco Bay Brand cysts. Cysts were obtained in 3.8-liter, vacuum-packed cans directly from the supplier (San Francisco Bay Brand, Inc., Newark, CA). Occasionally, smaller quantities in 75-g cans were purchased from local aquarium-supply stores. Once opened, the large cans were refrigerated and small quantities of cysts were withdrawn as needed. Cyst origins, lot numbers, or dates of purchase were not recorded or correlated with crab larval culture success.

Cysts used in 1978 and 1979 were San Francisco Bay Brand, obtained in 75-g vacuum-packed cans with lot numbers 1877 and 1628, respectively. In 1980 we used cysts from Brazil (Aqua fauna, Inc., Los Angeles, CA), lot number 501918.

Brine Shrimp Larval Hatching

Most brine shrimp nauplii were hatched from cysts using the standard technique of incubating cysts in seawater and concentrating newly-hatched nauplii with light. We incubated about 2 g of cysts in 28 C seawater held in a 3.8-liter

glass jar. Continuous aeration and illumination were supplied. After 24 hr, nauplii were concentrated with a unidirectional light (Fibre-lite) and siphoned into a 20 × 25-cm enamel pan, then into a screened-bottom (102- μ m Nitex), 15-cm-diameter container. They were rinsed with 1- μ m-filtered, UV-treated seawater for 20 min and held at a density of 200 nauplii per ml at ambient temperature (10–14 C). These nauplii were fed to crab zoeae usually within 24 hr of cyst hatch. They received a final rinse with ambient-temperature, filtered seawater prior to use. The fungicide Malachite Green (0.20 mg/liter) occasionally was added to the cyst-incubation jar to retard possible fungal infection of nauplii and subsequent infection of crab zoeae.

Crab zoeae raised in 1979 and 1980 were fed nauplii (from San Francisco Bay and Brazil cysts, respectively) obtained using the decapsulation technique for hatching brine shrimp cysts (Sorgeloos, et al. 1977). This is a two-step procedure that involves removing the hard outer layer (chorion) by hydrating cysts in a hypochlorite solution, then hatching them in seawater. Both decapsulation and hatching were done in a PVC-pipe section (25.4-cm high × 7.6-cm diameter). Aeration was introduced through a sealed threaded fitting at the bottom (Figure 118) to keep cysts in suspension.

Our decapsulation procedure entailed hydrating 20 g of cysts in a solution of 400-ml filtered seawater mixed with 400 ml of 5.25% commercial hypochlorite (bleach). Cysts were hydrated 1 hr in seawater, then 20 min in the hypochlorite solution. Decapsulated cysts were rinsed with seawater, dehydrated in a hyper-saline solution, and stored frozen in vials (2-g quantities).

To hatch decapsulated cysts, the contents of a single vial were thawed and poured into the 25.4-cm high (800-ml) PVC-pipe section. Cysts were incubated in filtered seawater at 27 C for 24 to 48 hr with continuous light and aeration. Contents were then poured into a 3.8-liter jar; nauplii were concentrated with a unidirectional light (Fibre-lite) and siphoned into a screened-bottom (102- μ m Nitex), 15-cm-diameter container. The remaining procedures for rinsing, storing, and feeding nauplii to crab zoeae were as previously described.

Brine Shrimp Adults

Live adult brine shrimp (San Francisco Bay Brand) were purchased weekly from a local aquarium supply store. These were maintained in an 8-liter, screened-bottom container with a continuous flow of filtered, UV-treated, ambient-temperature seawater. In 1979 and 1980, adult brine shrimp were treated routinely with the algacide Cutrine Plus (Applied Biochemists, Inc., Mequon, WI) at a concentration of 0.5 ppm for 24 hr as a retardant to biological fouling. After treatment, brine shrimp were rinsed thoroughly and fed to megalopae and postlarval crabs.

Results

Cyst Origin

San Francisco Bay cysts, purchased from 1971 through 1977, had variable hatching success. Usually hatches were satisfactory; however, an occasional "bad" hatch was encountered where all nauplii were dead and the cyst-incubation solution became putrid.

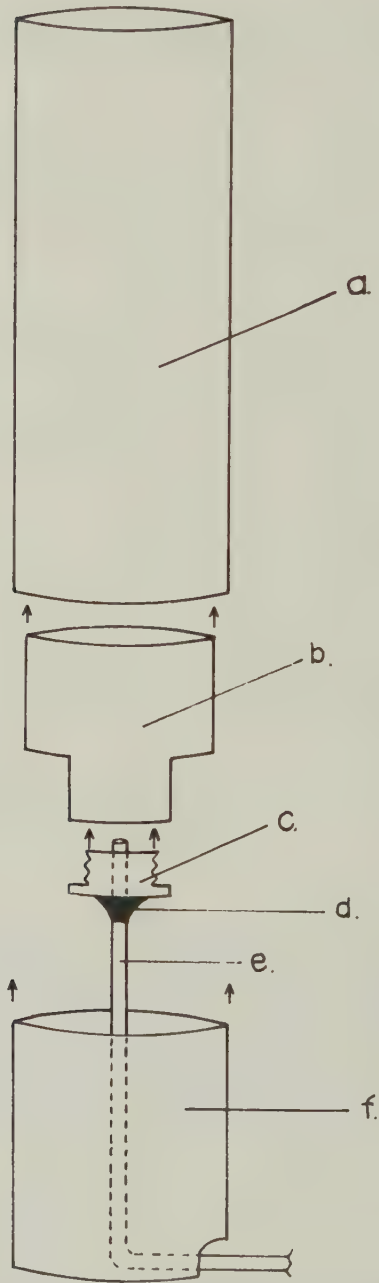


FIGURE 118. Decapsulation and cyst incubation chamber; a, PVC pipe section, 8.9 cm (od), 7.6 cm (id), 25.4 cm length; b, PVC reducer (slip $\times$ thread), 6.35 cm $\times$ 1.9 cm; c, threaded reducer, 1.9 cm $\times$ 0.32 cm; d, hot glue seal; e, air supply tubing, 0.32 cm; f, base.

During 1978 and 1979, San Francisco Bay cysts (lot number 1877 and 1628) produced satisfactory quantities of healthy nauplii. In 1980, Brazilian cysts also produced healthy nauplii, but hatching success was lower.

Brine Shrimp Larval Hatching

Using either procedure for producing nauplii, 2 g of cysts yielded about 2 liters of nauplii at a concentration of 200/ml. The standard hatching method (no decapsulation) yielded only moderately-clean nauplii, i.e., small quantities of unhatched cysts, cyst shells, and miscellaneous foreign material were present. Also, an occasional "bad" hatch was encountered. On the other hand, the decapsulation method (1979 and 1980) yielded a relatively clean naupliar hatch, and hatching success was consistent and satisfactory. Decapsulated cysts could be stored frozen up to 6 months without affecting hatching success, although hatching success was poor after 20 months.

The occasional practice of adding the fungicide Malachite Green to the incubation jar had no obvious effect and apparently was unrelated to the presence of the fungus *Lagenidium* sp. in crab zoeal cultures.

Brine Shrimp Adults

Fifty-seven grams of wet-packed brine shrimp were sufficient for feeding approximately 500 postlarval crabs (instars I through V) for 1 week. Treatment with the algacide Cutrine Plus greatly reduced fouling organisms (mainly filamentous bacteria) on adult brine shrimp. This treatment had no apparent deleterious effect on the brine shrimp or crabs that fed on these brine shrimp.

Discussion

It is possible that the origin of brine shrimp cysts (from different suppliers or different lot numbers from the same supplier) can influence cyst-hatching success, naupliar vigor, and subsequently zoeal culture success. However, we did not test for or observe an obvious relationship between these factors. Cysts from all origins had similar levels of external contaminants. Because the Brazilian cysts had a poorer hatch, we prefer those from San Francisco Bay. Cyst availability occasionally was a problem. In 1980, San Francisco Bay cysts were difficult to obtain in contrast to Brazilian cysts which were readily available.

The decapsulation technique for hatching brine shrimp cysts represents a distinct improvement in the overall methodology. Because this procedure removes external contaminants and results in clean naupliar hatches, it eliminates at least one potential zoeal-culture contamination source. However, the decapsulation technique does not eliminate possible "internal" problems, such as nutritional deficiencies (for zoeae) or chemical contamination (of the cysts).

There may be a relationship between brine shrimp cyst origin and the success of crab zoeal cultures; however, we did not test this possibility. Klein-MacPhee et al. (1982) found that the origin of cysts can be the determining factor in success or failure of laboratory animals, and Johns et al. (1980) found similar results with brachyuran crabs. Several research groups are presently standardizing lots of *Artemia* cysts for energy content and "hatching output" (Vanhaecke and Sorgeloos 1983).

Obtaining adult brine shrimp from an aquarium supply store is adequate for small-scale experiments, but because of high costs, other sources should be investigated if large quantities are needed. We briefly harvested adult brine shrimp from a local salt pond at Moss Landing, California. This was time consuming and brine shrimp were heavily fouled. We also attempted to raise adult brine shrimp from nauplii; however, this required extensive algal cultures (for food), space, and maintenance.

SUMMARY AND CONCLUSIONS

1. Adult ovigerous crabs, transported out of water, but maintained cool and moist, survive quite well without any apparent adverse effect on their developing embryos.
2. A nemertean worm, *Carcinonemertes errans*, was present in most egg masses. The role of this worm, relative to crab egg predation, and its possible effect on the crab resource is not fully understood.
3. Adult crabs readily mate in the laboratory and produce viable offspring. Our results suggest that the crab hatching period in the laboratory can be extended a few months beyond that occurring in the natural population.
4. An array of flask experiments was conducted to identify suitable culture criteria for crab zoeae. Flask-cultured zoeae generally showed very poor survival. Antibiotics or varied diets had little to no beneficial effect on zoeal survival in flasks.
5. A relatively successful, small-scale mass-culture apparatus was developed and tested for crab zoeae. Standard culture parameters were developed from an intensive series of trials with this apparatus. In the absence of a pathogenic fungus, zoeal culture success to the megalopal stage averaged 40%, while development time averaged 46 days. Inconsistencies in culture success with this apparatus could be traced to factors exogenous of the culture method.
6. A fungus, *Lagenidium* sp., gained entry to many zoeal cultures and resulted in moderate to extensive mortality. This fungus has been found on female crab egg masses and most likely is transmitted directly to crab larvae and consequently to our cultures. Efforts to prevent fungal entry to zoeal cultures were not successful.
7. Zoeal-stage spine breakage was a problem in both sand- and screen-substrate cultures and probably was a significant mortality factor. Spine breakage probably resulted from sudden lighting changes that caused zoeae to dart about and impact with culture container walls. A constant but subdued lighting source possibly would alleviate this problem.
8. Stunting of laboratory-cultured crabs, when compared to the natural population, first became evident in early zoeal stages and continued through the postlarval instars. This stunting may be related to diet or to physiological factors peculiar to the "artificiality" of cultivation.
9. Cannibalism first appeared at the megalopal stage (megalopae cannibalizing zoeae) and again became evident at postlarval instar III and older crabs (cannibalizing newly-molted, soft-shelled individuals). Instar III and later

stages must be cultured individually to prevent cannibalism. This is labor-intensive.

10. Megalopal culture success averaged 89%. An average of 22.9 days was required for megalopae to reach the first postlarval instar.
11. Postlarval instars were cultured on Nitex screen or sand substrate. Screen is recommended for the early instars, principally from a culture maintenance standpoint.
12. Brine shrimp naupliar hatching was refined via a decapsulation technique using a hypochlorite solution. These nauplii, hatched from cysts obtained from two geographical sources, proved a successful diet for zoeae.
13. Live adult brine shrimp from San Francisco Bay provided a successful diet for megalopae and early postlarval instars through instar V.
14. A diet of frozen squid was satisfactory for postlarval instars II and older. Fresh oyster was unsatisfactory.

Chapter 22

EFFECT OF SUBSTRATE TYPE ON SURVIVAL AND GROWTH IN HIGH DENSITY COMMUNAL CULTURES OF JUVENILE DUNGENESS CRABS, *CANCER MAGISTER*

BY

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INTRODUCTION

Large numbers of juvenile Dungeness crabs, *Cancer magister*, were maintained in individual cells at the Department of Fish and Game Marine Culture Laboratory (MCL) near Monterey for use in bioassays (Horne et al., Chapter 17; Haugen, Chapter 18). Culturing reptantians in individual cells is effective in minimizing mortalities but is highly labor intensive (Van Olst et al. 1976; Yamada 1977; Ebert et al., Chapter 21; etc.). The alternative, communal culturing, has been beset by problems of high mortality rates primarily due to cannibalism (e.g., Shleser and Tchobanoglous 1974; Welsh 1974; Van Olst et al. 1975). However, these studies indicate that different substrate types may have differing effects on survival and growth in communal cultures. Lobster survival was shown to be enhanced on substrates providing interstices, such as oyster shells, polyvinyl chloride (PVC) tubes, or rocks (Van Olst et al. 1975).

My study was conducted to assess the effects of three substrate types (sand, AstroTurf, and styrene) on survival and growth of juvenile Dungeness crabs in communal cultures as possible alternatives to individual culture. Although sand is the most "natural" substrate for wild Dungeness crabs (Waldron 1958), AstroTurf and styrene both require less maintenance and, given favorable survival and growth rates, would be preferred to sand.

In the study, juvenile crabs collected in the field were monitored for survival and growth on these three substrate types. In addition, crabs were maintained in individual cells as a control for background non-cannibalistic mortality.

MATERIALS AND METHODS

The juvenile Dungeness crabs used in this study were taken from Drake's Bay (Figure 11) by the Department of Fish and Game on June 28, 1977 using a small otter trawl aboard the RV KELP BASS. These animals were transferred live to the Marine Culture Laboratory where approximately 1000 were maintained individually in a "care-o-cell" system similar to that described by Van Olst et al. (1975).

For my experiment, 12 communal culture cells were constructed from 6-inch (152-mm) sections of PVC pipe with an inside diameter (id) of 6 inches (152 mm). These cells were set in three overflow trays on a water table. Three substrates, AstroTurf, styrene, and sand, were used in the cells, four replicate

cells of each substrate type, one substrate type per tray. Circles of AstroTurf and styrene were glued to the open bases of cells. The AstroTurf was marine surface type FH03, 100% polyethylene, made by Monsanto Co., St. Louis, MO 63166. Styrene substrate was from Penn Plax aquarium dividers. This material provides a smooth surface with 0.052-inch (1.3-mm) perforations spaced 0.18 inches (4.4 mm) apart. A bed of sand in one tray provided the sand substrate. The sand was obtained from a local beach, washed, and sieved to a uniform size of 0.052 to 0.092 inches (1.3 to 2.3 mm). A subsand filter was used to prevent fouling and clogging. The base of each sand-substrate cell was equipped with a 0.28-inch (7.1-mm) polyethylene mesh grid so that these cells could be pressed into and removed from the sand bed. This allowed for exposure, with minimal disturbance, of buried crabs and molts which were retained in the coarse mesh. These cells were pressed into the sand to a depth of about 1.25 inches (31.3 mm).

Individual "control" cells were constructed of 5-inch (127-mm) sections of 4-inch (102-mm) id PVC pipe initially divided into four compartments with thin sheets of styrene. The bases of these cells were equipped with 0.25-inch (0.6-mm) polyethylene mesh grid. As the crabs grew, one divider was removed to provide two larger compartments, and more cells were added as needed. These individual cells were maintained on the "care-o-cell" described by Yamada (1977).

Seawater, filtered to 15 μm and ultraviolet-treated, was supplied to communal and control cells at 17.0 ± 1.0 C (SD) and 17.1 ± 1.0 C (SD), respectively.

One month following their capture, I selected 350 juvenile crabs for this experiment. Three hundred were used in the communal cells. These were selected for uniformity in size, limb numbers, and synchrony of molting dates. Carapace widths (cw), excluding 10th anterolateral spines, ranged from 16.5 to 22.6 mm with a mean width of 19.4 ± 1.2 mm (SD), giving these animals an approximate age of instar IV (Collier, Chapter 10). All had molted within an 8-day period from July 14 to 22. Twenty-five were transferred at random from the pool of 300 into each cell giving an initial crab density of $7.3/\text{cm}^2$ ($1380/\text{m}^2$).

The 50 additional crabs were placed in individual cells in the small "care-o-cell." These animals were not selected for molt synchrony, but were of a size range similar to those in the communal cells with a mean carapace width of 19.6 ± 1.2 mm (SD).

Molting, limb loss, and mortality were monitored in all cells. Molts and dead individuals were removed and running totals of remaining crabs were tallied daily. Once each week a complete census was conducted in the communal cells in which crabs were individually enumerated, sexed, and their limbs counted. Regenerated limbs were counted as whole limbs. Limb counts in the control were made only during mid-intermolt periods in the communal cells.

The time interval (intermolt period) between successive molting periods in the communal cells was based on cell averages because communal culture did not allow keeping track of individual animals. Collection of molts and enumerating mortalities on a daily basis allowed computation of two average molting dates for each cell: (i) for all crabs molting and, (ii) for all crabs molting that would survive to the next molt. The difference between date (ii) for an initial molting period and date (i) for the following period approximated the average intermolt period. Thus, the intermolt period was the average time it took survivors of a given molt to reach the next molt.

Changes in size and intermolt duration were analyzed using two-way analysis of variance (ANOVA; Sokal and Rohlf 1969). Two-way nested ANOVA was used to compare survival between successive molting periods, substrates, and cells. These comparisons were based on a fixed ratio of surviving individuals per 15 crabs per cell initially. Each ratio was transformed using arc-sine^{-1} to avoid problems with normality using ratios.

Crabs in both communal and individual cells were fed market squid, *Loligo opalescens*. Frozen squid were thawed, diced, and fed on alternate days. Prior to each feeding, all remaining food was removed and the quantity fed adjusted to ensure that an excess remained at the next feeding. All of the communal cells received equal volumes of squid at each feeding.

The experiment ran for 92 days at which time a breakdown in the seawater system ended the experiment.

RESULTS

Molting Frequency

A total of three molting periods was completed in all substrates. A fourth molting period reached completion only in the sand substrate. During the first molting period, the number of molts counted in each of three substrates was less than the number of crabs initially available to molt. Thereafter, it was less than or more than the number available to molt (Table 75). About half of the "missing" molts were explained by hard-shelled mortalities not due to cannibalism. Thirteen of the "missing" molts could not be explained this way. Occasionally, crabs molted more than once during a given molting period, resulting in cumulative totals higher than the number of survivors from the previous molting period (styrene molting period two and sand molting period three; Table 75).

TABLE 75. Total Molts Counted and Number of Crabs Surviving Each Molting Period.

Substrate	Molting period					
	1		2		3	
	Total molts	Number of survivors	Total molts	Number of survivors	Total molts	Number of survivors
Styrene		16		10		6
		15		4		3
		16		4		2
		16		4		2
		—		—		—
Total	88	63	64	24	22	13
Artificial Turf		12		5		3
		14		8		4
		15		8		5
		12		7		3
		—		—		—
Total	91	53	49	28	27	15
Sand		10		5		3
		16		7		3
		13		5		3
		16		7		4
		—		—		—
Total	92	55	53	24	25	13

Mortality and Limb Loss

Mortalities were separated into two types, cannibalism and mortality due to other causes. Noncannibalistic mortalities invariably occurred to hard-shelled individuals. In the communal cells, the majority of such mortality occurred prior to the first molt. In the controls, these mortalities occurred more evenly throughout the experiment. Overall, hard-shelled mortalities were low for both the controls and substrates, ranging from 7 to 9% (Table 76).

TABLE 76. Hard-shell Mortality Not Due to Cannibalism.

Molting period	Control		Styrene		AstroTurf		Sand	
	Ratio	%	Ratio	%	Ratio	%	Ratio	%
1	1/50	2.0	7/100	7.0	4/100	4.0	5/100	5.0
2	0/49	0	1/63	1.6	2/53	3.8	2/55	3.6
3	2/45	0.4	0/22	0	1/28	3.6	0/24	0
4	1/41	4.4	1/13	7.7	0/15	0	0/13	0
Total	4/50	8.0	9/100	9.0	7/100	7.0	7/100	7.0

Cannibalism occurred in both the individual cells and the communal cultures. On three occasions escaped crabs from individual cells fell into an adjacent cell and were consumed by or consumed the cell mate. All cannibalism in communal cells apparently was on live soft-shelled individuals. All observed cases occurred within minutes after or during ecdysis when soft tissues were exposed. Just prior to molting, a crab assumed a defensive posture with claws extended and its vulnerable posterior carapace margin away from other crabs. Predatory crabs were often observed waiting for such an emerging individual. Crabs were cannibalized either while immobile during emergence, when the soft posterior carapace margin was exposed, or just after emergence during the instant it took to expand their limbs. The captured crabs' limbs were most often consumed first. If a crab was released or escaped prior to extensive carapace damage, it would often survive and be tallied as having undergone limb loss. With the exception of a low amount of limb loss as determined from the isolated controls, all limb loss apparently occurred from cannibalism.

In all three substrates, mortality was substantial during the first three molting periods (Table 75), primarily due to cannibalism. During the first molting period, crabs on styrene had the lowest mortality with 63 of 100 (63%) surviving, while on AstroTurf and sand, 53 and 55 of 100 (53 and 55%), respectively, survived. During the next molting period, 22 of 63 crabs (35%) survived on styrene, while on AstroTurf and sand, 28 of 53 (53%) and 24 of 55 (44%) survived. Survival in the third molting period on all three substrates was similar with 13 of 22 (59%) surviving on styrene, 15 of 28 (54%) on AstroTurf, and 13 of 24 (54%) on sand. Thus, near the end of this experiment, overall survival was similar for all substrates.

A fourth molt was not completed by all crabs on AstroTurf and styrene due to termination of the experiment, but for those crabs that did molt, mortality was substantially reduced. Highest survival was on styrene where 9 of 10 (90%) molted individuals survived with three crabs yet to molt. On AstroTurf, five of six (83%) survived with nine yet to molt. On sand, where all crabs completed their fourth molt, 9 of 13 (69%) survived.

The first three molting periods for all three substrates showed highly significant differences in survival ($P < 0.001$); there was, however, no significant difference between substrates. There was a significant "cell effect" ($P < 0.01$) reflecting some variation between cells.

Overall, survival rates (survival as a function of time) increased throughout the experiment. The slopes of the survival curves were asymptotic with mortality rates decreasing at lower crab densities (Figure 119).

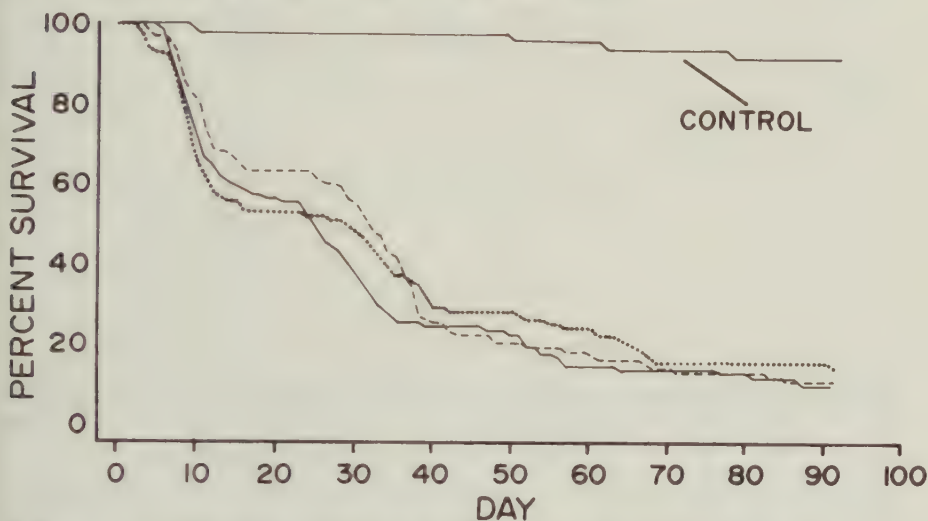


FIGURE 119. Crab survival versus days from onset of experiment. AstroTurf =; styrene = -----; sand = ———.

Intermolt Period

Crabs on the sand substrate underwent significantly shorter average intermolt periods than crabs on the other two substrates ($P < 0.001$). These crabs had a mean intermolt period of 19.8 days between molting periods one and two versus 22.9 and 23.1 days for crabs on AstroTurf and styrene, respectively (Table 77). The mean intermolt period between molting periods two and three for sand substrate animals averaged 23.3 days, also shorter than the 28.7 and 27.1 days for crabs on AstroTurf and styrene, respectively (Table 77). The mean intermolt period for all substrates was significantly longer for older crabs ($P < 0.001$).

Growth

Measurements of carapace widths showed differences in growth between molting periods and between substrates (Table 78). Initially, all crab widths were similar with sand substrate animals having an average size of 19.5 mm cw compared to 19.4 mm in styrene and AstroTurf. After the third molting period, the average size of crabs in the sand bed was 41.9 mm cw, over 3.5 mm larger than the average size of crabs on both styrene (38.3 mm) and AstroTurf (38.2 mm). The differences in growth between substrates and between molting periods were significant ($P < 0.01$ and 0.001, respectively).

TABLE 77. Average Length (in Days) of Intermolt Period by Substrate and Cell.

Substrate		Intermolt period	
		1	2
Styrene		23.6	28.9
		22.0	27.5
		22.0	24.9
		24.7	27.0
	Overall $\bar{x}$	23.1	27.1
AstroTurf		21.2	27.8
		23.1	28.0
		24.3	30.4
		23.0	28.6
	Overall $\bar{x}$	22.9	28.7
Sand		16.9	22.6
		21.7	21.3
		18.5	24.4
		22.6	24.7
	Overall $\bar{x}$	19.8	23.3

TABLE 78. Average Carapace Width (mm) of Crabs by Intermolt Period, Substrate, and cell.

Substrate		Intermolt period			
		0*	1	2	3
Styrene		19.0	24.0	29.7	37.9
		19.5	24.8	31.4	38.2
		19.6	24.4	31.3	40.7
		19.5	24.6	30.8	36.4
	Overall $\bar{x}$	19.4	24.5	30.8	38.3
AstroTurf		19.2	24.1	31.7	39.0
		19.1	24.0	30.7	37.0
		19.5	24.3	30.2	37.7
		19.7	25.5	31.6	39.2
	Overall $\bar{x}$	19.4	24.5	31.1	38.2
Sand		19.6	25.0	33.9	43.7
		19.1	24.4	30.2	41.7
		19.6	24.7	32.7	44.3
		19.6	25.4	31.2	37.7
	Overall $\bar{x}$	19.5	24.8	32.0	41.9

* Carapace widths at beginning of experiment.

DISCUSSION

There are three possible explanations for the lower number of molts enumerated at the end of a molting period compared to the number available to molt at the beginning. In addition to hard-shelled mortalities, crabs occasionally may delay molting for an entire molt. Also, molts occasionally may be consumed and it is possible that under the initial higher densities molts were consumed more rapidly and subsequently missed by the observer.

Mortality data from the first three molting periods indicate that survival of juvenile crabs in high density communal cultures on these substrates can be expected to be poor. The nonsignificant difference between substrates further indicates that, at these densities, none of the substrate types enhanced survival better than the others.

AstroTurf was chosen originally as a substrate with spacing between "grass blades" intended to reduce encounters between molting and non-molting crabs, thus reducing cannibalism. That this did not occur at the initially high densities I tested indicates that either the interstices were too small for the size range of crabs used, or AstroTurf may reduce a molting individual's mobility and avoidance of predation. Future experiments should utilize more varied substrates (e.g., broken shells, PVC tubes, etc.) or if this type of AstroTurf is utilized, smaller initial crab sizes should be tested. Although the percent mortalities were similar during the first three molting periods, as crabs grew intermolt periods increased in duration, spreading mortalities over a longer time. Thus, survival rates increased as crab density declined.

The higher survival in the fourth molting period needs to be interpreted cautiously because this molting period was incomplete for two of the substrates. However, the density of crabs was much reduced by then (180 to 270/m²) and the increase in survival may be attributable to these lower densities.

Van Olst et al. (1975) suggested claw loss in communal cultures of the American lobster resulted from agonistic (defensive or aggressive interaction) and not cannibalistic behavior. In my study, Dungeness crab limb loss (both claws and walking legs) apparently resulted primarily from cannibalism. The minimal loss in the controls suggests that only a small portion of the limb loss in the communal cells could be attributed to reasons other than cannibalism or possibly agonistic behavior.

Van Olst et al. (1975) found no significant difference in lobster growth between substrates. They attributed a small apparent difference in growth on sand substrate to a possible nutritional advantage of higher rates of cannibalism. In my study no such nutritional advantage could account for the more rapid growth of crabs on sand substrate because the incidence of cannibalism was similar in all substrates.

In the wild, Dungeness crabs are known to show a preference for sandy to sandy-mud bottoms, yet may be found on almost any type of bottom (Waldron 1958). A study to determine substrate preference of adult Dungeness crabs in the laboratory (Welsh 1974) indicated a behavioral preference for sand/shell substrate over sand or gravel. It seems possible that some nutritional and (or) behavioral response to a more natural substrate than styrene or AstroTurf could enhance growth rates in both size and molt periodicity.

Higher growth rates would have adaptive advantage to juvenile wild crabs since adult forms molt less frequently and have fewer predators. A more rapid growth to larger sizes would also be advantageous for mass culture purposes where a decrease in culturing time would decrease production and manpower costs.

I did not determine an optimal mass culture density because mortality rates did not level off substantially until the end of the experiment. My study does

suggest, as did Van Olst et al. (1975), that at lower stocking densities (< 300 crabs/m²) communal culture may be feasible when compared to the labor intensive individual culturing systems available. However, substantially larger numbers of animals would be required initially than for individual culturing.

Future studies should concentrate on lower stocking densities (< 300 crabs/m²) and different substrate types to assess optimal substrates for growth and molt periodicity, and to determine whether substrate type has any beneficial effect on reducing cannibalistic mortalities at these lower densities.

Chapter 23

SUMMARY AND RECOMMENDATIONS

by

PROGRAM STAFF

This chapter contains a brief and general overview of the life history of Dungeness crabs in central California, a section presenting the major findings relative to the decline and continued low level of the population, management options for improving the situation, and some suggestions for additional research.

LIFE HISTORY

The reproductive cycle in central California Dungeness crabs is completed annually once maturity has been reached (Figure 120). Mating occurs in the ocean, March through May, between hard-shelled males and recently molted, soft-shelled females. Sperm are stored internally until October–November when the eggs are extruded and fertilization occurs. After the eggs are extruded, the ovaries begin developing for the next cycle. From 1–2 million eggs are carried in a sponge-like mass on the female's abdomen until late December–mid January when most hatching takes place during a 2-week period.

The duration of the larval period (5 zoeal and 1 megalopal stages) ranges from approximately 105 to 125 days. Zoeae make vertical diel migrations in the water column and spend relatively more time in surface waters (darkness) than at 15–25 m (daylight); as a result early stage zoeae are transported offshore because of the seaward movement of surface waters. Late stage zoeae are found farther offshore than early stage zoeae and are probably carried northward by prevailing currents.

Young megalopae are found offshore in March but move toward the coast where ultimately more advanced stages are found aggregated nearshore in April. Megalopae generally are found within the upper 15 m of the water column, but the last developmental stages are also found near the bottom where molting to the first crab stage subsequently occurs.

Areas of substantial young-crab abundance are located where currents are likely to concentrate megalopae and entrain them until they are ready to settle out. Many crabs settling out in the vicinity of the entrance to San Francisco Bay enter the Bay system during May and June as a result of the influence of bottom currents and end up primarily in north San Francisco and San Pablo Bays. Zero-age class crabs become patchily distributed on the nursery grounds within the Bay and ocean. The nursery areas occupied by these crabs are similar in size for both locations.

Crabs grow by molting and Bay-reared crabs molt more frequently than ocean-reared crabs. Crabs leave the Bay after approximately 1 year, at or near sexual maturity (ca. 100 mm carapace width) and nearly twice the size of their ocean counterparts. Thus Bay-reared crabs are available to the males-only fishery at about 3 years of age and ocean-reared crabs at about 4 years.

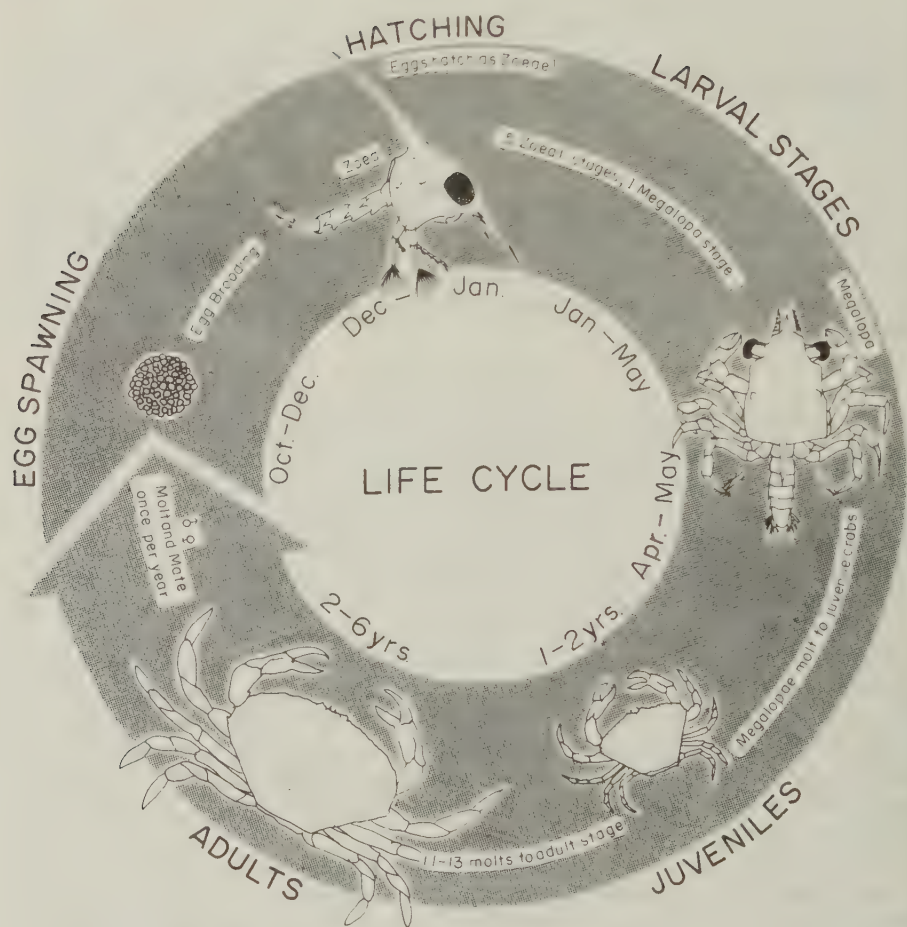


FIGURE 120. Life cycle of the Dungeness crab in California.

MAJOR RESEARCH RESULTS

The decline in the central California crab fisheries in the early 1960's closely followed a major change in the oceanographic climate in the late 1950's. The factors which appear to contribute to the sustained low levels of these fisheries include persistence of this change in oceanographic climate as well as the effects of predation and pollution.

Physical Oceanography—The evidence for the major cause of the decline in Dungeness crab fishery landings in central California points strongly to a major fluctuation in the ocean climate. The fluctuation, characterized by higher sea levels, included increases in water temperature and intensifications of the Davidson Current. Higher water temperatures may limit ovary development and have been shown to reduce egg survival and hatching success. Increased frequency of intensified Davidson Currents may have caused larvae to drift farther northward and decreased recruitment to central California.

Predation—Columbia River hatcheries began producing substantial numbers of silver salmon concurrent with the initial years of the decline and continue to do so. Many of these salmon are found along the central and northern California coast where they feed upon megalopae moving inshore. Predation on megalopae may account for significant reduction in recruitment to central California.

Our limited laboratory studies on the nemertean worm, *Carcinonemertes errans*, which are found in crab egg masses, have not shown any detrimental effect on the hatching success of crab eggs.

Pollution—Intense chlorination of San Francisco Bay wastewater began in the early 1960's and continued until the late 1970's. Laboratory exposure of juvenile Dungeness crabs to levels of chlorine residuals, comparable to and greater than estimated levels in the Bay during this time period, probably did not result in mortality but could have caused sublethal behavioral effects. Virtually all wastewater currently discharged into the Bay is dechlorinated.

We cannot assess the effects that toxic trace elements, including heavy metals, may have had on the central California crab population during the decline; however, laboratory tests showed that 96-hour exposure to each of three elements, at higher than ambient levels, were lethal to Dungeness crabs. Sixty-day tests for sublethal effects at lower concentrations were less conclusive.

Analyses of juvenile and adult crab tissues between 1973 and 1975 for chlorinated pesticides and PCB content indicated that the levels were not obviously detrimental to those stages' survival.

Juvenile Dungeness crabs in the San Francisco Bay complex contain higher tissue burdens of hydrocarbons (saturated and unsaturated oils, including petroleum compounds) than their Eureka counterparts, indicating a potential pollution stress. The sediments in the Bay complex contain numerous polynuclear aromatic hydrocarbons (PAH); these are among the most toxic components of petroleum. However, crabs from the Bay did not show detectable accumulation of PAH from the sediments. This lack of accumulation of the most toxic fraction of sediment pollutant hydrocarbons may indicate that the crabs are able to metabolize them to other compounds which we did not measure, or that there is little uptake of them by the crabs.

Since our limited pollution work was completed the scope of knowledge about pollutants and their effects has increased. Therefore, the possible influence of pollutants on the crab population should continue to be investigated.

Mariculture—The full life cycle of the Dungeness crab was completed in the laboratory. Moreover, crab mating and spawning were effected out-of-phase with the natural population. This has value for possible experimental and enhancement efforts. Three major culture problems were identified, namely, (i) infection by a highly virulent pathogenic fungus *Lagenidium* sp. that caused extensive larval mortalities, (ii) larval stunting, and (iii) post-larval cannibalism. Stunting is probably linked to nutritional deficiency. Efforts to treat or eliminate the fungus in our cultures were not successful. The fungus was present on egg-bearing female crabs from the natural population. However, its extent and transmission routes in the natural population are unknown. We speculate that, because of its pathogenicity in laboratory cultures, the fungus could be a contributing factor to the decline of the central California Dungeness crab fishery. Cannibalism became extensive in juvenile communal cultures at crab instar III and could not be controlled except by isolation of crabs in individual cells. This proved highly labor intensive.

MANAGEMENT OPTIONS

We feel that if any or all of the following options are exercised, there will be a net benefit to the Dungeness crab resource in the San Francisco area and may result in increased commercial landings:

1. Develop and conduct an action program to implement enhancement techniques based on feasibility and cost-benefit studies. Some techniques to be examined include the following: (i) artificial rearing and seeding of larval or juvenile crabs out of phase with the local population; (ii) relocation of Gulf larvae to avoid losses due to predation; (iii) collection of larvae from northern California for introduction into central California; (iv) introduction of larval crabs into areas where losses due to currents would be reduced; and (v) seeding of juvenile crabs into under-utilized portions of the Bay.
2. Eliminate commercial trawl fishing in critical areas of the Gulf of the Farallones during periods of peak molting (July–September) for male Dungeness crabs.
3. Permit commercial trawl activities and eliminate commercial Dungeness crab fishing in the nearshore (within 3 miles) area between Pt. Bonita and Bodega Head during March only. Trawling would remove predators (e.g., starry flounder) from an area where substantial numbers of megalopae settle in April. Marketable sized flatfish can be found in this area which has approximately 100 miles² of trawlable bottom. There would be little negative impact on Dungeness crab and California halibut resources. Closing of this limited fishery prior to March 31st should be an option of Northern Ocean Management Unit Three if monitoring (including fish stomach analysis) indicates early settlement of megalopae, and (or) a significant impact on soft female crabs.
4. Establish a legal size for females and permit the retention and sale of females for a 4-year trial period. This could increase the yield of the fishery by up to 5%. The positive effect of decreasing cannibalism on early juvenile instars and the negative effect of reduced reproduction are undetermined but considered minimal.
5. Implement the self-destruct device regulation (Fish and Game Code No. 9000.5) for commercial crab traps. Each year approximately 10% of the crab traps fished are lost. Although the extent of crab mortality due to these lost traps has not been determined, destruct devices that would decompose within a specified period of time would allow for the escape of captured crabs.
6. Require two 4³/₈-inch escape ports in commercial crab traps, with a time lock on their use. Such a requirement would increase escapement of sublegal male crabs from 57 to 83% and escapement of females from 51 to 70%. This change from the current 4¹/₄-inch escape ports would not result in the escapement of any significant number of legal-sized crabs.

The need to protect juvenile Dungeness crab nursery areas in central California should be a vital part of any management plan. Appropriate agencies must be encouraged to monitor and enforce water quality standards in the San Francisco Bay complex and nearshore ocean areas and prohibit loss of habitat.

RESEARCH NEEDS

As a result of our Program and the efforts of other investigators, much has been learned about the Dungeness crab in California; however, research often generates as many questions as answers. The following is a list of needs we feel additional research could and should satisfy for a more comprehensive understanding of this valuable resource:

1. Determine origin, route, and transport mechanisms of megalopae arriving at the central California coast.
2. Conduct northern California studies to determine relative fecundity, spawning stock, larval abundance, and megalopa-juvenile crab relationships, and the relative importance of the latter to the commercial fishery.
3. Determine causes of accelerated growth rate in San Francisco Bay-reared crabs.
4. Obtain quantitative data on the relationship of silver salmon production, their predation on megalopae, and recruitment of megalopae to central California.
5. Conduct further studies on relationships between Dungeness crab eggs and the nemertean worm *Carcinonemertes errans*.
6. Conduct laboratory studies on long-term and synergistic effects of pollutants on Dungeness crabs.
7. Conduct laboratory studies to resolve problems of fungus *Lagenidium* sp. infection and stunting in mass cultivation of Dungeness crab eggs, larvae, and juveniles.
8. Determine the incidence and transmission routes of the fungus *Lagenidium* sp., and its relationship to the health and stability of the central California Dungeness crab population.

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APPENDIX I

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Leo Singer

¹ Listed Alphabetically Within Organization, Agency, or Unit

APPENDIX I—Continued

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Gary Paoli, Bill Waters

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Martindale, and crew

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Bob Grossi, Fred Kemp, and crew

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Joe Brown
Don Carvalho
Ken Croney
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Nep Escalante
Joe Falcone
Andy Felando
Bill Hinz
Henry Iverson
Jim Knox
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Frank McCumisky
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Dick Fenner
Lee Miller
Dan Odenweller
Don Stevens
Santos Tobar

*ANADROMOUS FISHERIES
BRANCH**Eureka*

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Gail Campbell

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Terry Lambert

APPENDIX I—Continued

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John Snodgrass and crew of RV
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APPENDIX I—Continued**CENTRAL WASHINGTON STATE COLLEGE**

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TEXAS A. & M. UNIVERSITY

Guritno Roesijadi

ALASKA DEPARTMENT OF FISH AND GAME

Jerry McCrary

WASHINGTON DEPARTMENT OF FISHERIES

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PLANNING STUDY, MENLO PARK**

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GROUP, MONTEREY**

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Dale Bretschneider

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Doug McLain

Craig Nelson

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Gunter Seckel

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Pete Benville

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Gregory Lough

CANADA DEPARTMENT OF FISHERIES AND OCEANS**PACIFIC BIOLOGICAL STATION, NANAIMO, B. C.**

Terry Butler

**INTER-AMERICAN TROPICAL TUNA COMMISSION,
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BODEGA BAY

Earl Carpenter

SAN FRANCISCO

Tony Casale

Robert Miller

HALF MOON BAY

Bill Genochio

APPENDIX I—Continued**BULLETIN REVIEW**

This Bulletin was reviewed and critiqued among members of the Dungeness Crab Research Program. In addition, primary overall reviewers were Terry Butler (Canada Department of Fisheries and Oceans), Herb Frey, John Geibel, Dan Gotshall, and Hal Orcutt (California Department of Fish and Game). Selected chapters were reviewed by Earl Ebert, Larry Espinosa, Art Haseltine, and Mike Martin (CDFG); Andy Bakun and Dick Parrish (National Marine Fisheries Service, Pacific Environmental Group); Bill Peterson (State University of New York at Stony Brook); and Elizabeth Venrick (University of California San Diego, Scripps Institute of Oceanography).

APPENDIX II

Coordinates for All Ocean Stations Sampled, 1975-1980

Station	Latitude	Longitude	Station	Latitude	Longitude
784	37° 35'30"N	122° 42'30"W	1128	37° 44'30"N	122° 53'30"W
816	37° 36'30"N	122° 41'30"W	1138	37° 44'30"N	123° 03'30"W
824	37° 36'30"N	122° 49'30"W	1151	37° 45'30"N	122° 34'30"W
838	37° 37'30"N	122° 30'30"W	1153	37° 45'30"N	122° 36'30"W
864	37° 37'30"N	122° 56'30"W	1159	37° 45'30"N	122° 42'30"W
873	37° 38'30"N	122° 30'30"W	1160	37° 45'30"N	122° 43'30"W
874	37° 38'30"N	122° 31'30"W	1161	37° 45'30"N	122° 44'30"W
906	37° 38'30"N	123° 03'30"W	1163	37° 45'30"N	122° 46'30"W
917	37° 39'30"N	122° 38'30"W	1165	37° 45'30"N	122° 48'30"W
947	37° 40'30"N	122° 31'30"W	1167	37° 45'30"N	122° 50'30"W
948	37° 40'30"N	122° 32'30"W	1169	37° 45'30"N	122° 52'30"W
950	37° 40'30"N	122° 34'30"W	1173	37° 45'30"N	122° 56'30"W
957	37° 40'30"N	122° 41'30"W	1191	37° 46'30"N	122° 30'55"W
961	37° 40'30"N	122° 45'30"W	1192	37° 46'30"N	122° 31'30"W
975	37° 40'30"N	122° 59'30"W	1195	37° 46'30"N	122° 34'30"W
979	37° 40'30"N	123° 03'30"W	1196	37° 46'30"N	122° 35'30"W
993	37° 41'30"N	122° 38'30"W	1198	37° 46'30"N	122° 37'30"W
1002	37° 41'30"N	122° 47'30"W	1199	37° 46'30"N	122° 38'30"W
1006	37° 41'30"N	122° 51'30"W	1201	37° 46'30"N	122° 40'30"W
1007	37° 41'30"N	122° 52'30"W	1204	37° 46'30"N	122° 43'30"W
1011	37° 41'30"N	122° 56'30"W	1216	37° 46'30"N	122° 55'30"W
1024	37° 42'30"N	122° 30'30"W	1236	37° 46'30"N	123° 15'30"W
1030	37° 42'30"N	122° 36'30"W	1241	37° 47'30"N	122° 29'30"W
1033	37° 42'30"N	122° 39'30"W	1242	37° 47'30"N	122° 30'30"W
1042	37° 42'30"N	122° 48'30"W	1245	37° 47'30"N	122° 33'30"W
1050	37° 42'30"N	122° 56'30"W	1248	37° 47'30"N	122° 36'30"W
1052	37° 42'30"N	122° 58'30"W	1251	37° 47'30"N	122° 39'30"W
1053	37° 42'30"N	122° 59'30"W	1259	37° 47'30"N	122° 47'30"W
1056	37° 42'30"N	123° 02'30"W	1274	37° 47'30"N	123° 02'30"W
1057	37° 42'30"N	123° 03'30"W	1291	37° 48'30"N	122° 29'30"W
1064	37° 43'30"N	122° 30'40"W	1294	37° 48'30"N	122° 32'30"W
1068	37° 43'30"N	122° 34'30"W	1295	37° 48'30"N	122° 33'30"W
1069	37° 43'30"N	122° 35'30"W	1296	37° 48'30"N	122° 34'30"W
1071	37° 43'30"N	122° 37'30"W	1297	37° 48'30"N	122° 35'30"W
1072	37° 43'30"N	122° 38'30"W	1299	37° 48'30"N	122° 37'30"W
1086	37° 43'30"N	122° 52'30"W	1300	37° 48'30"N	122° 38'30"W
1087	37° 43'30"N	122° 53'30"W	1332	37° 48'30"N	123° 10'30"W
1090	37° 43'30"N	122° 56'30"W	1342	37° 49'20"N	122° 29'30"W
1092	37° 43'30"N	122° 58'30"W	1343	37° 49'20"N	122° 30'30"W
1093	37° 43'30"N	122° 59'30"W	1347	37° 49'30"N	122° 34'30"W
1094	37° 43'30"N	123° 00'30"W	1350	37° 49'30"N	122° 37'30"W
1100	37° 43'30"N	123° 06'30"W	1352	37° 49'30"N	122° 39'30"W
1108	37° 44'30"N	122° 33'30"W	1353	37° 49'30"N	122° 40'30"W
1111	37° 44'30"N	122° 36'30"W	1357	37° 49'30"N	122° 44'30"W
1113	37° 44'30"N	122° 38'30"W	1383	37° 49'30"N	123° 10'30"W
1116	37° 44'30"N	122° 41'30"W	1390	37° 49'30"N	123° 17'30"W
1118	37° 44'30"N	122° 43'30"W	1398	37° 50'30"N	122° 35'30"W
1120	37° 44'30"N	122° 45'30"W	1399	37° 50'30"N	122° 36'30"W
1123	37° 44'30"N	122° 48'30"W	1400	37° 50'30"N	122° 37'30"W
1127	37° 44'30"N	122° 52'30"W	1404	37° 50'30"N	122° 41'30"W

APPENDIX II—Continued

Coordinates for All Ocean Stations Sampled, 1975–1980

<i>Station</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Station</i>	<i>Latitude</i>	<i>Longitude</i>
1406	37° 50'30"N	122° 43'30"W	3035	37° 35'20"N	123° 14'50"W
1407	37° 50'30"N	122° 44'30"W	1950	38° 02'30"N	123° 05'30"W
1414	37° 50'30"N	122° 51'30"W	1983	38° 03'30"N	123° 03'30"W
1448	37° 51'20"N	122° 34'30"W	2022	38° 04'30"N	123° 06'30"W
1450	37° 51'30"N	122° 36'30"W	3030	37° 37'55"N	123° 09'10"W
1451	37° 51'30"N	122° 37'30"W	3040	37° 32'55"N	123° 20'15"W
1472	37° 51'30"N	122° 58'30"W	3045	37° 30'10"N	123° 25'30"W
1478	37° 51'30"N	123° 04'30"W	3050	37° 27'50"N	123° 31'10"W
1503	37° 52'30"N	122° 39'30"W	3060	37° 22'35"N	123° 42'15"W
1510	37° 52'30"N	122° 46'30"W	3070	37° 17'20"N	123° 53'25"W
1529	37° 52'30"N	123° 05'30"W	3080	37° 12'10"N	124° 04'30"W
1540	37° 52'30"N	123° 16'30"W	3090	37° 06'55"N	124° 15'35"W
1550	37° 53'30"N	122° 38'30"W	3100	37° 01'45"N	124° 26'40"W
1551	37° 53'30"N	122° 39'30"W	3230	37° 44'20"N	123° 21'00"W
1552	37° 53'30"N	122° 40'30"W	3235	37° 41'50"N	123° 26'20"W
1560	37° 53'30"N	122° 48'30"W	3240	37° 39'20"N	123° 31'50"W
1561	37° 53'30"N	122° 49'30"W	3245	37° 37'00"N	123° 37'10"W
1571	37° 53'30"N	122° 59'30"W	3250	37° 34'25"N	123° 42'45"W
1584	37° 53'20"N	123° 12'30"W	3260	37° 29'15"N	123° 53'30"W
1607	37° 54'30"N	122° 47'30"W	3270	37° 24'05"N	124° 04'15"W
1639	37° 54'30"N	123° 19'30"W	3280	37° 18'55"N	124° 15'00"W
1652	37° 55'30"N	122° 46'30"W	3290	37° 13'50"N	124° 25'45"W
1657	37° 55'30"N	122° 51'30"W	3300	37° 08'40"N	124° 36'30"W
1660	37° 55'30"N	122° 54'30"W	3425	37° 56'25"N	123° 32'50"W
1694	37° 56'20"N	122° 46'40"W	3430	37° 56'10"N	123° 39'10"W
1698	37° 56'30"N	122° 50'30"W	3435	37° 55'50"N	123° 45'20"W
1701	37° 56'30"N	122° 53'30"W	3440	37° 55'30"N	123° 51'45"W
1709	37° 56'30"N	123° 01'30"W	3445	37° 55'15"N	123° 58'00"W
1727	37° 56'30"N	123° 19'30"W	3450	37° 54'55"N	124° 04'20"W
1734	37° 56'30"N	123° 26'30"W	3601	38° 18'10"N	123° 02'20"W
1736	37° 57'30"N	122° 47'30"W	3602	38° 14'15"N	123° 06'25"W
1747	37° 57'30"N	122° 58'50"W	3603	38° 13'25"N	123° 02'55"W
1756	37° 57'30"N	123° 07'30"W	3604	38° 12'30"N	123° 00'00"W
1757	37° 57'30"N	123° 08'30"W	3605	38° 09'05"N	123° 04'35"W
1762	37° 57'30"N	123° 13'30"W	3606	38° 08'10"N	123° 01'30"W
1763	37° 57'30"N	123° 14'30"W	3607	38° 07'25"N	122° 58'40"W
1769	37° 57'30"N	123° 20'30"W	3611	38° 17'25"N	123° 05'55"W
1784	37° 58'30"N	122° 55'30"W	3616	38° 17'25"N	123° 12'15"W
1800	37° 58'30"N	123° 11'30"W	3621	38° 17'25"N	123° 18'35"W
1804	37° 58'30"N	123° 15'30"W	3626	38° 17'20"N	123° 25'00"W
1819	37° 59'30"N	122° 50'30"W	3631	38° 17'20"N	123° 31'25"W
1836	37° 59'30"N	123° 07'30"W	3636	38° 17'20"N	123° 37'45"W
1851	37° 59'30"N	123° 22'30"W	3701	38° 19'15"N	123° 05'45"W
1852	37° 59'30"N	123° 23'30"W	3705	38° 20'20"N	123° 10'20"W
1862	38° 00'30"N	122° 53'30"W	3710	38° 21'45"N	123° 16'25"W
1864	38° 00'30"N	122° 55'30"W	3715	38° 23'15"N	123° 27'45"W
1865	38° 00'30"N	122° 56'30"W	3860	39° 04'50"N	125° 00'25"W
1908	38° 01'30"N	123° 00'30"W	3870	39° 06'10"N	125° 13'10"W
1945	38° 02'30"N	123° 00'30"W	3880	39° 07'20"N	125° 26'30"W

APPENDIX II—Continued

Coordinates for All Ocean Stations Sampled, 1975–1980

Station	Latitude	Longitude	Station	Latitude	Longitude
3890	39° 08'40"N	125° 39'20"W	4480	40° 53'00"N	126° 03'15"W
3900	39° 10'00"N	125° 52'15"W	4490	40° 56'20"N	126° 15'40"W
3905	39° 06'35"N	123° 48'55"W	4500	40° 59'40"N	126° 28'10"W
3910	39° 07'15"N	123° 55'25"W	4505	40° 36'15"N	124° 27'30"W
3915	39° 08'00"N	124° 01'40"W	4510	40° 38'00"N	124° 33'35"W
3920	39° 08'45"N	124° 08'10"W	4515	40° 39'50"N	124° 39'30"W
3925	39° 09'30"N	124° 14'35"W	4520	40° 41'40"N	124° 45'35"W
3930	39° 10'10"N	124° 21'00"W	4525	40° 43'25"N	124° 51'45"W
3935	39° 10'55"N	124° 27'20"W	4530	40° 45'15"N	124° 57'30"W
3940	39° 11'45"N	124° 33'40"W	4535	40° 47'10"N	125° 03'40"W
3945	39° 12'30"N	124° 40'15"W	4540	40° 49'00"N	125° 09'55"W
3050	39° 13'15"N	124° 46'35"W	4545	40° 50'45"N	125° 15'45"W
3960	39° 14'45"N	124° 59'10"W	4550	40° 52'45"N	125° 22'15"W
3970	39° 16'10"N	125° 11'50"W	4560	40° 56'30"N	125° 34'40"W
3980	39° 17'40"N	125° 24'30"W	4570	41° 00'10"N	125° 46'50"W
3990	39° 19'15"N	125° 37'10"W	4580	41° 03'50"N	125° 59'20"W
4000	39° 20'40"N	125° 50'00"W	4590	41° 07'30"N	126° 11'20"W
4010	39° 14'10"N	123° 58'40"W	4600	41° 10'50"N	126° 23'30"W
4020	39° 21'15"N	124° 07'45"W	4605	40° 45'25"N	124° 20'20"W
4030	39° 28'10"N	124° 17'05"W	4610	40° 44'50"N	124° 26'45"W
4110	39° 46'05"N	124° 04'55"W	4615	40° 44'20"N	124° 33'25"W
4120	39° 40'40"N	124° 16'40"W	4620	40° 43'45"N	124° 40'00"W
4130	39° 35'10"N	124° 26'15"W	4625	40° 43'10"N	124° 46'30"W
4205	39° 47'45"N	123° 56'20"W	4701	40° 57'10"N	124° 49'10"W
4210	39° 49'10"N	124° 02'40"W	4702	40° 55'20"N	124° 43'40"W
4220	39° 51'45"N	124° 15'00"W	4703	40° 53'40"N	124° 38'25"W
4230	39° 54'25"N	124° 27'25"W	4704	40° 51'50"N	124° 32'50"W
4240	39° 57'00"N	124° 39'45"W	4705	40° 50'15"N	124° 27'45"W
4250	39° 59'35"N	124° 52'30"W	4706	40° 48'30"N	124° 22'20"W
4305	40° 31'30"N	124° 30'25"W	4707	40° 46'35"N	124° 18'00"W
4315	40° 23'00"N	124° 36'25"W	4805	40° 56'00"N	124° 14'35"W
4320	40° 18'30"N	124° 39'25"W	4808	40° 55'40"N	124° 18'35"W
4330	40° 09'30"N	124° 44'50"W	4814	40° 54'55"N	124° 26'25"W
4405	40° 27'25"N	124° 31'15"W	4820	40° 54'15"N	124° 34'30"W
4410	40° 29'15"N	124° 37'25"W	4825	40° 53'45"N	124° 41'10"W
4415	40° 30'50"N	124° 43'30"W	4901	40° 48'45"N	124° 40'15"W
4420	40° 32'35"N	124° 49'35"W	4902	40° 51'10"N	124° 31'00"W
4425	40° 34'20"N	124° 55'55"W	4903	40° 52'45"N	124° 22'10"W
4430	40° 36'05"N	125° 02'00"W	4904	40° 54'25"N	124° 13'30"W
4435	40° 37'50"N	125° 08'10"W	5000	39° 25'30"N	123° 49'30"W
4440	40° 39'30"N	125° 14'15"W	5001	39° 25'30"N	123° 50'30"W
4445	40° 41'15"N	125° 20'00"W	5002	39° 27'30"N	123° 53'30"W
4450	40° 43'00"N	125° 25'45"W	5003	39° 26'30"N	123° 54'30"W
4460	40° 46'20"N	125° 38'10"W	5004	39° 25'30"N	123° 55'30"W
4470	40° 49'40"N	125° 50'30"W	5005	39° 22'30"N	123° 52'30"W

APPENDIX II—Continued

Coordinates for All Ocean Stations Sampled, 1975–1980

<i>Station</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Station</i>	<i>Latitude</i>	<i>Longitude</i>
5006	39° 19'30"N	123° 54'30"W	5028	39° 24'30"N	123° 51'30"W
5007	39° 22'30"N	123° 53'30"W	5029	39° 28'30"N	123° 52'30"W
5009	39° 21'30"N	123° 51'30"W	5030	39° 30'30"N	123° 55'30"W
5010	39° 17'30"N	123° 52'30"W	5031	39° 30'30"N	123° 57'30"W
5011	39° 16'30"N	123° 52'30"W	5032	39° 30'30"N	123° 54'30"W
5012	39° 14'30"N	123° 52'30"W	5033	39° 30'30"N	123° 52'30"W
5013	39° 13'30"N	123° 50'30"W	5034	39° 31'30"N	123° 50'30"W
5014	39° 14'30"N	123° 50'30"W	5036	39° 28'30"N	123° 50'30"W
5015	39° 19'30"N	123° 51'30"W	5037	39° 24'30"N	123° 50'30"W
5016	39° 18'30"N	123° 51'30"W	5038	39° 21'30"N	123° 50'30"W
5017	39° 20'30"N	123° 51'30"W	5039	39° 20'30"N	123° 50'30"W
5018	39° 23'30"N	123° 51'30"W	5040	39° 30'30"N	123° 50'30"W
5026	39° 21'30"N	123° 52'30"W	5041	39° 23'30"N	123° 50'30"W
5027	39° 22'30"N	123° 51'30"W			

77701.....	GF	8	15	78	29	8	212
78101.....	GF	15	8	78	29	177	20,070
78801.....	GF	8	7	78	29	8	944
78802.....	GF	7	7	78	29	7	478
78104.....	GF	14	8	58	22	142	21,663
78401.....	EK	6	31	58	22	6	691
78503.....	GF	31	11	58	22	73	10,837
78505.....	GF	33	8	58	22	33	4,370
78516.....	GF	8	7	58	22	8	1,044
79401.....	GF	7	7	58	22	7	600
79201.....	GF	7	7	58	22	7	671
79402.....	EK	10	10	58	22	10	1,360
79801.....	GF	5	5	58	22	5	533
79202.....	GF-EK	3	48	2	2	146	28,694
79503.....	GF-BB	43	7	2	2	84	19,842
79203.....	GF	7	7	2	2	7	807
80201.....	GF	8	8	2	2	8	826
80202.....	GF	4	4	2	2	8	628
80401.....	EK	4	4	2	2	4	417
80203.....	FB	15	7	2	2	22	2,709
80204.....	GF-BB	12	13	3	8	44	6,427
80205.....	FB	28	11	3	8	39	5,432

* See Appendix II.

† Collected by Marine Resources Region.

APPENDIX V

Bay Plankton Tow Summary, 1975-1979

Areas sampled are San Francisco Bay estuarine complex (SF) and Humboldt Bay (HB); tow types are horizontal and oblique; all net diameters are 0.5 m; mesh sizes are 0.343, 0.505, and 1.0 mm.

Cruise code *	Area	Horizontal			Oblique			Total no. tows	Total volume water filtered (m ³)
		0.343	0.505	1.00	0.343	0.505	1.00		
75505	SF	14	-	-	22	-	-	36	5,665
75506	SF	2	-	-	11	-	-	13	2,016
75507	SF	7	-	-	8	-	-	15	2,400
76901	SF	-	-	-	6	-	-	6	666
76902	SF	-	-	-	6	-	-	6	726
76903	SF	-	-	-	6	-	-	6	726
76301	SF	-	20	-	-	7	-	27	2,457
76507	SF	-	-	-	-	15	-	15	1,383
76508	SF	-	6	-	-	11	-	17	1,874
77102	SF	-	-	-	-	4	-	4	612
77602	SF	-	-	-	-	9	-	9	675
77104	SF	-	-	-	-	4	-	4	413
77105	SF	-	4	-	-	4	-	8	1,054
77503	SF	-	-	-	-	15	10	25	1,914
†	HB	-	-	-	-	1	-	1	46
78101	SF	-	-	-	-	8	-	8	932
78104	SF	-	-	-	-	6	-	6	338
78503	SF	-	-	-	-	-	10	10	1,474
78505	SF	-	-	-	-	5	-	5	402
79503	SF	-	-	6	-	-	17	23	6,718

* See Appendix II

† Sampled From Shore

APPENDIX VI

Station Locations for Shore-based Ringnet Survey.

<i>Code</i>	<i>Station no.</i>	<i>Location</i>
PTCH	503	Port Chicago, U.S. Naval Weapons Station tug boat dock
BNCA	500	City of Benicia, boat launching facility
CRKT	078	Crocket, Dowrelio's fishing pier
PLMA	014	Petaluma River, Sonoma County boat launching facility
LCLD	130	Loch Lomond Marina, San Rafael
VNPR	106	Valley Nitrogen Producers, Hercules, water intake pier
PNPT	116	Pinole Point fishing pier, East Bay Regional Park District
PPRK	180	Paradise Park fishing pier, Marin County Park District
RDRK	153	Red Rock Marina, Castro Point Pier, Richmond
FTBR	228	Ft. Baker fishing pier, Golden Gate National Recreational Area
BERK	214	City of Berkeley, fishing pier or marina
MUNI	243	Municipal pier, City of San Francisco
CAND	305	Candlestick Point, ferry pier
SHBT	421	Channel overpass near Showboat restaurant, Burlingame
SEXP	278	Sea Explorers pier, Ballena Yacht Club, Alameda
SNMT	422	San Mateo County, fishing pier
SNLO	330	City of San Leandro, fishing pier
RDCY	472	Port of Redwood City, commercial dock

APPENDIX VII

Fishes Sampled for Stomach Contents, 1975-1980

Scientific name	Common name	Ocean		Bay	
		Number examined	Number with food	Number examined	Number with food
<i>Acipenser medirostris</i> *	green sturgeon	1	1	7	7
<i>Acipenser transmontanus</i> *	white sturgeon	1	1	9	7
<i>Alosa sapidissima</i>	American shad	-	-	1	-
<i>Amphistichus rhodoterus</i> *	redtail surfperch	1	1	1	1
<i>Anoplopoma fimbria</i>	sablefish	3	2	-	-
<i>Artedius notospilotus</i>	bonyhead sculpin	-	-	1	1
<i>Atheresthes stomias</i>	arrowtooth flounder	1	-	-	-
<i>Chilara taylori</i>	spotted cusk-eel	2	2	-	-
<i>Chitonotus pugetensis</i>	roughback sculpin	2	2	-	-
<i>Citharichthys sordidus</i> *	Pacific sanddab	132	71	-	-
<i>Clupea harengus</i>	Pacific herring	4	4	-	-
<i>Damalichthys vacca</i> *	pile surfperch	12	9	39	29
<i>Embiotaca lateralis</i>	striped surfperch	1	1	-	-
<i>Engraulis mordax</i>	northern anchovy	2	2	-	-
<i>Eopsetta jordani</i>	petrale sole	41	30	-	-
<i>Genyonemus lineatus</i> *	white croaker	91	73	194	172
<i>Glyptocephalus zachirus</i> *	rex sole	123	101	-	-
<i>Hemilepidotus spinosus</i> *	brown Irish lord	1	1	-	-
<i>Hexagrammos decagrammus</i> *	kelp greenling	8	8	-	-
<i>Hydrolagus collieri</i>	rat fish	4	4	-	-
<i>Hyperprosopon anale</i> *	spotfin surfperch	6	4	-	-
<i>Hyperprosopon argenteum</i>	walleye surfperch	-	-	3	2
<i>Hyperprosopon ellipticum</i>	silver surfperch	-	-	1	1
<i>Hypsopsetta guttulata</i>	diamond turbot	-	-	14	9
<i>Hypsurus caryi</i>	rainbow surfperch	1	1	-	-
<i>Lepidopsetta bilineata</i> *	rock sole	24	20	-	-
<i>Leptocottus armatus</i> *	staghorn sculpin	52	43	234	178
<i>Lyopsetta exilis</i>	slender sole	12	10	-	-
<i>Merluccius productus</i> *	Pacific hake	59	45	-	-
<i>Microgadus proximus</i> *	Pacific tomcod	91	84	41	39
<i>Microstomus pacificus</i>	Dover sole	56	52	-	-
<i>Mustelus henlei</i> *	brown smoothhound	17	14	144	139
<i>Myliobatis californica</i> *	bat ray	3	2	3	2
<i>Oncorhynchus kisutch</i> *	silver salmon	40	33	-	-
<i>Oncorhynchus tshawytscha</i> *	king salmon	45	24	-	-
<i>Ophiodon elongatus</i>	lingcod	36	23	2	2
<i>Otophidium scrippsi</i>	basketweave cusk-eel	1	-	-	-
<i>Paralichthys californicus</i>	California halibut	24	8	2	1

APPENDIX VII—Continued

Fishes Sampled for Stomach Contents, 1975–1980

Scientific name	Common name	Ocean		Bay	
		Number examined	Number with food	Number examined	Number with food
<i>Parophrys vetulus</i> *	English sole	201	177	18	16
<i>Peprillus simillimus</i>	Pacific butterfish	2	—	—	—
<i>Phanerodon furcatus</i> *	white surfperch	11	8	11	11
<i>Platichthys stellatus</i> *	starry flounder	144	115	185	162
<i>Pleuronichthys decurrens</i>	curlfin turbot	22	18	1	1
<i>Pleuronichthys verticalis</i>	hornyhead turbot	8	5	—	—
<i>Porichthys notatus</i>	plainfin midshipman	23	9	42	19
<i>Psetichthys melanostictus</i>	sand sole	60	35	3	2
<i>Raja binoculata</i> *	big skate	79	74	46	45
<i>Raja rhina</i>	longnose skate	5	4	—	—
<i>Rhacochilus toxotes</i> *	rubberlip surfperch	5	5	4	4
<i>Roccus saxatilis</i>	striped bass	—	—	14	8
<i>Scorpaenichthys marmoratus</i> *	cabezon	10	9	1	1
<i>Sebastes auriculatus</i>	brown rockfish	45	28	3	1
<i>Sebastes caurinus</i> *	copper rockfish	5	3	—	—
<i>Sebastes elongatus</i>	greenstriped rockfish	8	3	—	—
<i>Sebastes goodei</i>	chilipepper	2	1	—	—
<i>Sebastes helvomaculatus</i>	rosethorn rockfish	5	4	—	—
<i>Sebastes jordani</i>	shortbelly rockfish	1	—	—	—
<i>Sebastes levis</i>	cowcod	1	—	—	—
<i>Sebastes melanops</i> *	black rockfish	19	12	—	—
<i>Sebastes mystinus</i>	blue rockfish	1	1	—	—
<i>Sebastes paucispinis</i>	bocaccio	12	7	—	—
<i>Sebastes pinniger</i> *	canary rockfish	5	5	—	—
<i>Sebastes rosenblatti</i> *	greenblotched rockfish	2	1	—	—
<i>Sebastes ruberrimus</i>	yelloweye rockfish	1	—	—	—
<i>Spirinchus starksi</i> *	night smelt	9	3	—	—
<i>Squalus acanthias</i>	spiny dogfish	23	12	19	13
<i>Thaleichthys pacificus</i>	eulachon	3	1	—	—
<i>Triakis semifasciata</i> *	leopard shark	1	1	18	16
<i>Zalembius rosaceus</i>	pink surfperch	6	4	—	—
<i>Zaniolepis latipinnis</i>	longspine combfish	6	6	—	—

* Dungeness crab(s) present.

APPENDIX VIII Coordinates, Depth, and Loran (9940-C) for Crab Trawl Study Stations, July–September 1980

Date	Tow no.	Start			Stop				
		Latitude	Longitude	Depth (m)	Loran	Latitude	Longitude	Depth (m)	Loran
JUL	9	37°39'38"N	122°33'50"W	26	43154	37°49'30"N	122°40'36"W	26	43210
	9	37°45'20"N	122°38'02"W	20	43187	37°39'37"N	122°33'48"W	26	43154
	3	37°39'48"N	122°40'36"W	37	43159	37°45'18"N	122°45'00"W	38	43190
	6	37°45'18"N	122°45'00"W	40	43190	37°39'12"N	122°42'30"W	42	43157
	5	37°41'05"N	122°38'25"W	29	43165	37°47'21"N	122°39'24"W	24	43198
	6	37°47'21"N	122°39'24"W	24	43198	37°41'05"N	122°38'25"W	30	43165
	7	37°40'16"N	122°40'16"W	35	43161	37°47'21"N	122°39'24"W	26	43198
	7	37°44'40"N	122°38'54"W	27	43184	37°37'42"N	122°36'06"W	31	43145
	9	37°39'15"N	122°38'52"W	35	43155	37°46'34"N	122°41'32"W	33	43195
	10	37°46'34"N	122°41'32"W	33	43195	37°39'15"N	122°38'52"W	35	43155
AUG	3	37°37'22"N	122°35'40"W	31	43143	37°43'57"N	122°40'44"W	31	43181
	5	37°38'50"N	122°35'48"W	30	43151	37°44'18"N	122°40'12"W	31	43183
	3	37°39'47"N	122°33'38"W	26	43155	37°44'42"N	122°38'54"W	27	43184
	4	37°40'18"N	122°33'38"W	24	43157	37°44'54"N	122°38'21"W	22	43186
	5	37°44'22"N	122°44'10"W	37	43185	37°49'25"N	122°37'40"W	20	43209
	3	37°45'04"N	122°45'27"W	44	43189	37°50'00"N	122°38'54"W	26	43212
	6	37°50'24"N	122°44'54"W	35	43216	37°55'42"N	122°50'35"W	44	43245
	6	37°52'06"N	122°46'08"W	40	43225	37°57'41"N	122°52'36"W	40	43255
	7	37°39'12"N	122°36'28"W	30	43153	37°43'24"N	122°44'06"W	37	43180
	7	37°38'22"N	122°35'26"W	30	43148	37°44'18"N	122°40'12"W	31	43183
SEP	3	37°38'42"N	122°33'46"W	27	43150	37°44'42"N	122°38'54"W	28	43184
	9	37°37'40"N	122°36'06"W	31	43145	37°45'06"N	122°37'56"W	20	43185
	9	37°44'06"N	122°44'42"W	40	43184	37°49'25"N	122°37'40"W	20	43209
	8	37°44'36"N	122°45'58"W	44	43187	37°50'00"N	122°38'54"W	26	43212
	7	37°46'15"N	122°40'30"W	27	43193	37°52'07"N	122°46'18"W	42	43226

* Tow No. 1 was reset due to shipping traffic and is thus longer.